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SAND-HILL VEGETATION OF NORTHEASTERN COLORADO

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INTRODUCTION

The sand areas of Colorado include many districts of a few square miles in the plains region, and also certain smaller stretches in the higher valleys and mountain parks. Those somewhat fully studied by the writer are as follows: Roggen and northwest of Roggen, in Weld County; various eastern parts of the state, especially Washington, Sedgwick, and Yuma counties; White Rocks and Gunbarrel Hill in eastern Boulder County; Utah Junction and Globeville, respectively at the north and northeast city limits of Denver. Additional areas of sand in other parts of Colorado examined are: the eastern part of the San Luis Valley in Saguache County, with the Great Sand Dunes (Ramaley, 1929), Clear Creek Valley near Georgetown, Clear Creek County (Ramaley, 1919); the sand dunes of North Park in Grand County, the sand dunes of the Arkansas Valley in southeastern Colorado, especially in the neighborhood of Lamar.

It is natural to make comparisons with the sand hills of Nebraska, so well known because of their great extent, occupying about 20,000 square miles in the west-central part of the state. They have been described by Rydberg (1895), Pound and Clements (1900), and Pool (1914), the last-named giving a full discussion of physiography, climatology, and floristics. Since the sand hills of northeastern Colorado lie only 100 to 300 miles west of the sand-hill area in Nebraska, it is to be expected, and it actually is the fact that there is great similarity both ecologically and floristically in the two areas. Similarities and differences are pointed out in later sections of this present paper.

Among the most satisfactory for study are the sand hills to the north and west of Roggen, in Weld County, where they exhibit the features of true dunes (Fig. 1). Others are near Brush, Otis, and Akron. Not any of them are of great height, 50 feet at Roggen, seldom 100 feet anywhere in northeastern Colorado. Crater-like depressions, "blow-outs," occur on northwest exposures, and there is much loose sand, especially in "deposit patches" to the lee of blow-outs. Elsewhere in many parts of eastern Colorado visited by the writer there are fewer recently formed craters, and most of the sand hills are composed, at least superficially, of sandy loam or sandy clay, and support a somewhat stable, although meagre, vegetation.

This introduction would not be complete without reference to the kindness of Dr. Arthur G. Vestal who examined and made comments upon the table of successions (Fig. 10) and with whom the writer has discussed

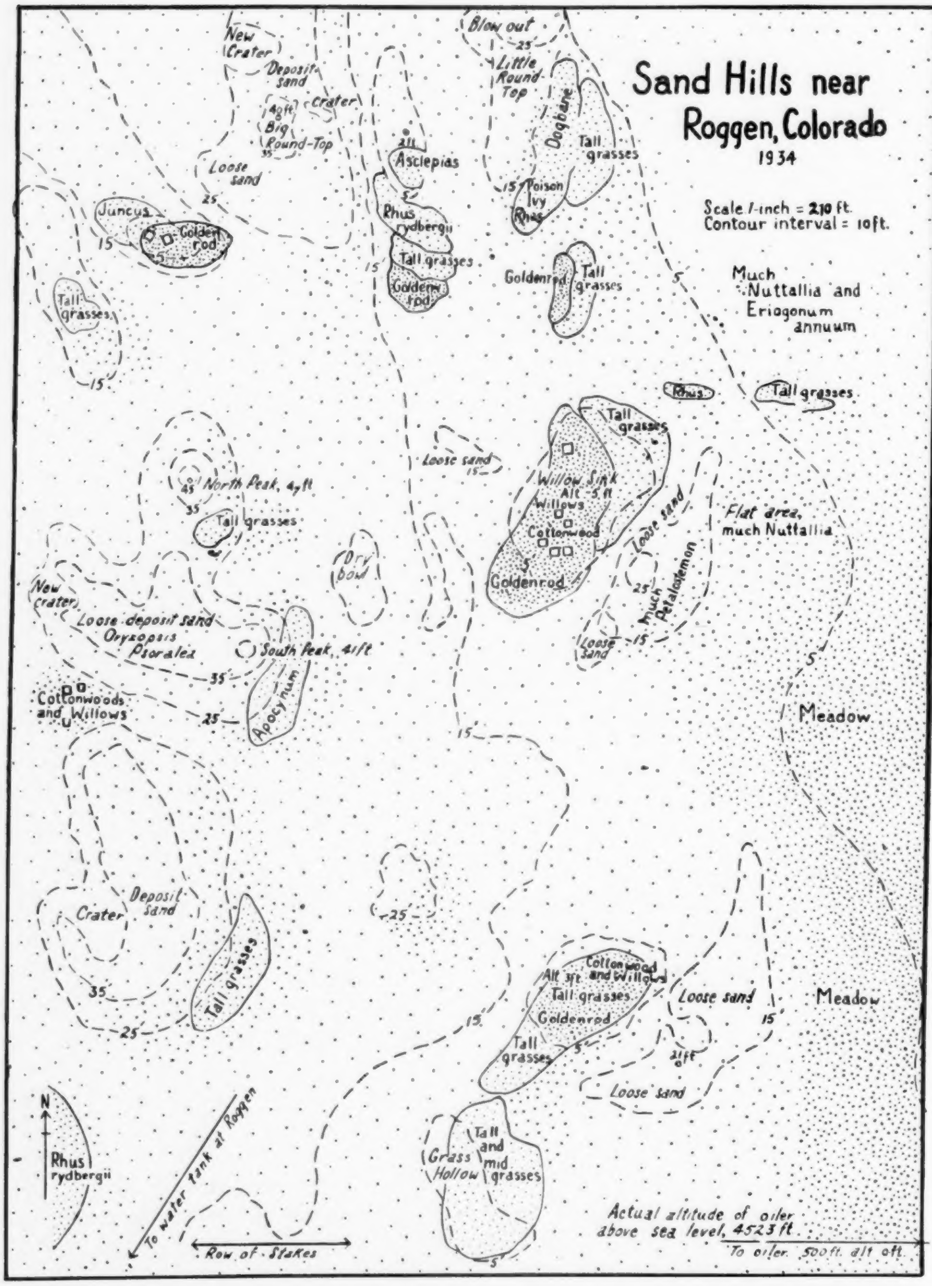

FIG. 1. Vegetation map of a typical part of the sand hills area 4 miles northeast of Roggen, Weld County, Colorado, Sec. 21, T. 3 N., R. 62 W. of 6th principal meridian; 55 miles east of the foothills at Boulder. A cattle oiler 500 feet east of the southeast corner of the mapped area was taken as the base station with altitude of 0 feet. The highest hill is 47 feet. An intermittent and sluggish stream, about 400 feet beyond the east boundary of the map, flows in a northerly direction. Density of vegetation is indicated by closeness of dots in stippling. The general sand-hills-mixed vegetation appears somewhat evenly distributed, but careful examination clearly shows scattered islands of tall grasses, *Juncus ater*, *Apocynum hypyericifolium*, and *Rhus rydbergii* usually on east slopes. Willows and cottonwoods are confined to sinks; goldenrods occur only in low and level areas. This map was begun in 1932 and completed in 1934.

many ecological problems. Dr. Raymond J. Pool has given me information concerning pioneer species in the Nebraska sand hills (Table 4). Much use has been made also of his excellent account (Pool, 1914).

CLIMATOLOGY

The climate of the sand hills areas in northeastern Colorado may be judged from the records of Denver, Greeley, Ft. Morgan, and Akron, all within 100 miles of the more typical sand hills. The mean July temperature is about 72 degrees Fahrenheit, with hot days often above 90 degrees and cool nights with the minimum often as low as 55 or 60 degrees. The mean annual rainfall is 12 to 13 inches, but precipitation in dry years may not be above 8 inches. Light afternoon showers, sometimes very light, are frequent in June and July. In the more eastern part of Colorado, where there are also sand hills, precipitation is close to 18 inches, but with the higher summer temperature (74.8 for July at Wray, Colorado) semi-arid conditions also prevail.

Evaporation is high, no doubt much higher than at Ft. Collins where Hanson, Love, and Morris (1931) found it to average 29 cc. daily during July from Livingston standardized cylindrical atmometers. At Boulder, 60 miles west of the nearest dunes, the writer found the evaporation from cylindrical atmometers to average 48 cc. daily in August, 1935; this, however, in a very dry period.

The heaviest winter winds are from the northwest, and these are the winds which produce craters, or blow-outs, and cause extensive movement of sand. Besides these, there are at all seasons the familiar mountain-and-valley winds, from the east during the day and from the west at night, with a certain amount of north and south wind chiefly at sunrise and sunset. Summer winds are usually light, and true sand storms are unknown at that season, but dust storms occur in dry periods. These are due to occasional long-continued south and southeast winds which blow up dust from southeastern Colorado and from Kansas, Oklahoma, and Texas.

SOILS

The soils of upland areas are moderately coarse, loose, silicious sand with no pebbles or rocks, and a minimum of loam. In valleys and sinks the addition of silt and organic matter gives the soil some compactness, and leads to stabilization. Plants of this finer-grained soil may form stands of considerable density, as in "hay meadows" of grasses, sedges, and rushes.

Upland soils are dry at the surface, but in years of normal rainfall are moist to the touch at a depth of a few inches. The water table of gently rolling ground in spring and early summer is at about 8 feet, while in mixed grass and sedge meadow it may be only 5 or 6 feet, and where salt grass and Scirpus grow it is still closer to the surface. Upland soils are slightly acid, those of low valleys and sinks are moderately alkaline. Chemical composition is doubtless similar to that of Nebraska sand hills (Pool, 1914).

Soil temperatures.—Readings of soil temperatures have been made during the months of June, July, August, and September of three different years. The highest temperature recorded is 130 degrees Fahrenheit, at the soil surface. Surface temperatures of 100 or more are common at mid-day through the growing season. Soil temperatures 12 inches below the surface vary from 70 to 80 during July and August throughout the sand-hills-mixed community. In the Solidago and Stipa communities they are consistently lower by 2 to 5 degrees.

Water content of soils.—Soil samples taken from June to September in different years show at both 6 inches and at 12 inches a low water content in the xeric communities. Usually the moisture in the first few inches is less than 1 per cent, often no moisture can be detected in surface soil; soon after a rain it may be as high as 3 per cent. In marsh communities the percentage is from 5 to 30.

Soil reaction.—Soil samples have been tested many times with the Youden hydrogen-ion concentration apparatus. To save printing a long table it may be briefly stated that records for upland soils are most often 6.8 or 6.9; in the *Panicum virgatum* society, 8.2; in the *Scirpus americanus* community, 8.6; and in the "sinks" with *Solidago canadensis,* 9.8.

Wilting Coefficient.—Samples of upland soil from the sand-hills-mixed community placed in glass tumblers were planted October 10, 1931 with barley, using the wax-seal method to prevent surface evaporation. After permanent wilting of the seedlings, some three weeks later, the water content was determined, showing wilting coefficients of four samples as follows: (1) 0.4 per cent; (2) 0.6 per cent; (3) 0.8 per cent; (4) 0.9 per cent.

Hygroscopic Coefficient.—Oven-dried soil was exposed for four days to saturated air under a bell jar. The following percentages were obtained. Upland soil of loose sand and blow-out community: sample (a) 0.8, (b) 1.8, (c) 1.4. Soil of sand prairie (Stipa community): (d) 3.4, (e) 3.6.

Mechanical analysis.—Samples which had been oven-dried were sifted to determine the percentages of the different soil-particle sizes. Particles which pass through a sieve of 60 meshes to an inch the writer calls *very fine;* those which pass a 40-mesh screen but not a 60-mesh screen are *fine;* those which pass a 20-mesh but not a 40-mesh are *medium;* those which do not pass the 20-mesh are *coarse.* In all of the samples the coarse material, so far as distinguishable, consists of plant and animal remains, especially seeds, bits of dry fruits and stems, and insect parts. Table 1 shows great similarity in most of the soils, but soil of the loose sand and blow-out community has the least fine material, and has much more of the medium-sized sand than the others. Soil of sand sage and sand prairie, as would be expected because of the protection by vegetation cover, has a larger proportion of very fine particles than the soil of the more primitive plant communities. An analysis of the sand of the Great Sand Dunes National Monument of southern Colorado is introduced in the table for comparison. This soil resembles

TABLE 1. MECHANICAL ANALYSIS OF SOILS OF COLORADO SAND HILLS
EACH RECORD THE AVERAGE OF TWO OR MORE SAMPLES (percentages)

	Very fire	Fine	Medium	Coarse	Total
Loose sand and blow-out community (Roggen)	12.8	33.1	52.0	2.1	100.0
Sand-hills-mixed (Roggen)	12.5	61.6	24.8	1.5	100.4
Sand-hills-mixed (Brush)	24.2	58.2	17.0	0.5	99.9
Sand sage (Brush)	31.2	41.4	26.5	1.3	100.4
Sand prairie (Roggen)	31.7	45.0	21.6	1.5	99.8
Great Sand Dunes of Southern Colorado	14.2	56.5	28.0	1.0	99.7

closely that of the sand-hills-mixed community of our area, yet it supports a much more meagre vegetation because of high winds, extreme insolation, and short growing season.

PHYSIOGRAPHIC PLANT ECOLOGY

The topography of the sand-hills area presents at least seven rather distinct habitats for plants, and the plant population responds by differences in floristic composition.

a. *Blow-outs and loose sand.*—Blow-out craters are usually situated near the tops of northwest hill slopes, and the loose sand which has been blown out accumulates on the lee side of the hill chiefly near the top (Fig. 4). Such bare places may remain devoid of vegetation for many years after their formation or after enlargement of a crater during a windy winter. The first plants are *Oryzopsis hymenoides, Cristatella jamesii,* and *Polanysia trachysperma* (Capparidaceae), *Phaca longifolia, Psoralea lanceolata, Heliotropium convolvulaceum.*

b. *Typical unstable sand hills.*—Covering hillsides and slopes there is a very open stand of "sand-hills-mixed" vegetation dominated by *Muhlenbergia pungens* and *Psoralea lanceolata* in the looser soil, with additional grasses and flowering herbs where some admixture of loam produces a slight degree of soil compactness (Figs. 2, 3, 4, 5, 8, 9). In more level areas the sand sage, *Artemisia filifolia,* is abundant and may even dominate the community (Figs. 6, 9).

c. *Stabilized hills.*—The older sand hills in which clay is present with the sand have vegetation somewhat different from that of the unstable sand hills. Many of the same species occur, but more xeric grasses are now frequent, as Aristida, Agropyron, Bouteloua, and Buchloe; and there are some flowering herbs which do not occur in more sandy soil (Fig. 7). These stabilized hills are not considered "typical" sand hills, and are only briefly considered in this paper.

FIG. 2. General view of sand hills near Roggen, Colorado in late summer of 1936; there were no conspicuous flowering herbs at the time. A patch of tall grasses, *Panicum virgatum* and *Andropogon hallii*, is near the front of the picture.

FIG. 3. Another part of the sand-hills area near Roggen, Colorado in June, 1937, showing typical appearance of the vegetation. A recently produced blow-out is seen. The sparse vegetation is chiefly *Muhlenbergia pungens* and *Psoralea lanceolata*.

FIG. 4. A crater of loose sand showing some scattered pioneer plants: *Heliotropium convolvulaceum* (white blossoms), *Psoralea lanceolata, Cristatella jamesii, Chamaesyce serpens.* Sunflowers are seen at the top of the ridge.

FIG. 5. Scene among the sand hills. The sand-hills-mixed vegetation covers the hills and the level areas, but there is everywhere considerable bare ground. At the right is a depression with willows, cottonwoods, and tall grasses.

FIG. 6. Sand sage community *(Artemisia filifolia)*, on level ground of sand-hills area near Brush, Colorado, September 15, 1937. Sand sage forms a somewhat permanent community partly dependent for its persistence upon grass fires and over-grazing. The soil is more compact than that which supports sand-hills-mixed vegetation. Back of the sand sage, on sloping ground, is the Muhlenbergia-Psoralea community.

FIG. 7. Somewhat stabilized sand hills south of Otis, Colorado, June 1937. The hillside supports a sparse growth of *Muhlenbergia pungens, Psoralea lanceolata, Buchloe dactyloides* and *Bouteloua gracilis* with scattered clumps of *Yucca glauca* and few xeric herbs. At the foot of the hill are shrubs of sand sage, and a single Yucca plant is in the foreground.

FIG. 8. A sandy slope near Roggen, Colorado, June, 1937. Vegetation chiefly *Muhlenbergia pungens*, which is at this time only about 3 inches tall. The plants of this bunch grass often grow in the form of rings or crescents.

FIG. 9. Sand hills 4 miles south of Brush, Colorado, September, 1937. The hill-top is loose sand with *Oryzopsis hymenoides* the characteristic plant, while the lower slope bears chiefly *Muhlenbergia pungens*. In the foreground, in more compact soil, there are scattered plants of *Artemisia filifolia*, the sand sage.

d. *Level upland areas with firmer yet sandy soil.*—Level upland areas commonly support a sand prairie in which *Stipa comata* and *Calamovilfa longifolia* are the most conspicuous grasses but where other grasses are numerous, and the proportion of flowering herbs is large.

e. *Depressions.*—There exist numerous undrained depressions, or sinks, in the wettest of which near the center cat-tails and bulrushes are present, encompassed by circum-areas of goldenrod and tall grasses. In some, a few willows and cottonwoods occur (Fig. 5). Dryer depressions have the center filled with goldenrod.

f. *Streams and banks.*—Small streams in various parts of the sand-hills area have a growth of algae, water-plantain, and arrowheads, while the banks support sedges, grasses, rushes, and such flowering herbs as buttercups, umbellifers, and spearmint.

g. The usually small streams of sand-hills country sometimes form rather level valleys varying in width from a few hundred feet to a half-mile, or more. Such valleys are occupied by meadow grassland. They furnish the ranchers with a supply of native hay, and are often called "hay meadows."

PLANT COMMUNITIES

Sand-hills vegetation develops on deep sandy soil which retains precipitation and has little run-off; it thus contains many deep-rooted species of grasses and other herbs, so that in favorable situations it approaches in appearance the prairies of the Mississippi valley, whereas in the more usual fine-grained, hard-baking soils of northeastern Colorado the vegetation is largely of short grasses, Bouteloua and Buchloe, with flowering herbs also low-growing and of a more xeric type than in sandy soil.

The sandy-soil communities here considered are represented by patches of various extent which are separated by more extensive short-grass plains or, since the coming of the white man, by cultivated, often irrigated, fields. Indeed, the sand hills of Colorado and their accompanying sand prairies are but scattered tracts of a few square miles, and in no case do they cover entire counties as do the sand hills of Nebraska.

SAND PRAIRIE COMMUNITY

The most advanced vegetation in the sand-hills area is the sand-prairie, a western extension of the prairies of Illinois, Iowa, and eastern Nebraska. This may be called Stipa-Andropogon-Calamovilfa Consociation. It is the final stage of a series of changes starting either in loose sand or in water of small ponds, sloughs, and slow-running streams.

As would be expected because of the arid climate, sandy soil, and high winds the upland vegetation is sparse, with much bare ground, and species are few in number. It is only in edaphically favored places that closed communities exist, that is, on level or gently rolling ground with soil having a

moderate amount of humus, and with the water-table near enough to the surface but not too near. Such areas are not extensive, although following slow physiographic changes they continue to develop in low places, through drainage of marshland. The meagre rainfall, high daytime temperatures, and high evaporation rate, however, will always keep the final stage of vegetation semi-xeric. There can be no luxuriant prairie, and the inevitable lowering of the water-table due to the various activities of man will tend to make all vegetation less mesophytic.

The chief plant communities of the sand hills are given in the following list. The order in succession is roughly as here indicated, but some of the stages may be, at times, omitted. In the detailed account, which follows the list, sand prairie is first described, then the members of the xerarch and the hydrarch series which lead to it are considered in order. The dominants of each community are given here in parenthesis.

Xerarch series:

Loose sand and blow-outs *(Oryzopsis hymenoides)*
Sand-hills-mixed *(Muhlenbergia pungens)*
Sand sage community *(Artemisia filifolia)*
Sand prairie *(Stipa-Andropogon-Calamovilfa)*

Hydrarch series:

Pondweed-arrowhead community *(Potamogeton-Sagittaria)*
Cat-tail-bulrush swamp *(Typha-Scirpus)*
Streambank community *(Equisetum-Berula-Mentha)*
Sedge-rush marshland *(Carex-Juncus)*
Willow-poplar community *(Salix-Populus)*
Grass meadow *(Agropyron-Hordeum-Panicum)*
Sand prairie *(Stipa-Andropogon-Calamovilfa)*

A chart, suggesting graphically the stages of progress in both xerosere and hydrosere, follows the detailed account of communities.

SAND PRAIRIE

Dominant species:

Stipa comata
Andropogon hallii
Calamovilfa longifolia

Important species:

Agrostis hyemalis
Agropyron pseudorepens
Agropyron smithii
Andropogon scoparius
Koeleria cristata
Panicum virgatum
Poa interior
Poa pratensis
Sporobolus cryptandrus
Delphinium virescens
Peritoma serrulatum
Helianthus petiolaris

Frequent species:

Agrostis alba
Agropyron dasystachyum
Elymus canadensis
Panicum scribnerianum
Carex heliophila
Carex eleocharis
Cyperus schweinitzii
Tradescantia occidentalis
Yucca glauca
Chenopodium oblongifolium
Argemone intermedia
Glycyrrhiza lepidota
Petalostemon villosus
Tithemalus robustus
Nuttallia stricta
Oreocarya suffruticosa
Aster multiflorus
Aster fluviatilis
Cirsium plattense
Machaeranthera ramosa
Solidago canadensis

Other species:

Agrostis hyemalis
Agropyron inerme
Agropyron pauciflorum
Aristida fendleriana
Bouteloua gracilis
Buchloe dactyloides
Festuca octoflora
Hordeum pusillum
Munroa squarrosa
Allium textile
Sisyrinchium occidentale
Eriogonum effusum
Eriogonum microthecum
Atriplex canescens
Cycloloma atriplicifolium
Corispermum nitidum
Salsola pestifer
Acnida tamariscena
Amaranthus spinosus
Abronia elliptica
Lesquerella argentea
Amorpha fruticosa
Lupinus pusillus
Parosela lanata
Petalostemon oligophyllus
Petalostemon compactus
Sophora sericea
Tium drummondii
Vicia sparsifolia
Linum lewisii
Croton texensis
Gaura coccinea
Gaura parviflora
Sphaeralcea coccinea
Meriolix serrulata
Acrolasia albicaulis
Eustoma russellianum
Apocynum hypericifolium
Acerates angustifolia
Acerates viridiflora
Asclepias arenosa
Asclepias speciosa
Cuscuta indecora
Evolvulus nuttallianus
Ipomoea leptophylla
Cryptanthe fendleri
Lappula occidentalis
Lithospermum angustifolium
Lithospermum canescens
Gilia longiflora
Gilia polyantha
Microsteris micrantha
Phlox depressa
Phlox planitiarum
Phlox scleranthifolia
Monarda pectinata
Scutellaria brittonii
Physalis heterophylla
Physalis longifolia
Linaria canadensis
Pentstemon albidus
Pentstemon angustifolius
Pentstemon secundiflorus
Mysorrhiza multiflora
Thalesia fasciculata
Plantago purshii
Symphoricarpos symphoricarpos
Artemisia frigida
Artemisia gnaphalodes
Aster multiflorus
Chrysopsis foliosa
Chrysopsis villosa
Chrysothamnus spp.
Cirsium megacephalum

Cirsium plattense
Erigeron pumilus
Grindelia erecta
Gutierrezia sarothrae
Hymenopappus tenuifolius
Machaeranthera tanacetifolia
Senecio densus
Sideranthus spinulosus

In this and other lists, plants are arranged by families in the Engler and Prantl sequence, but genera in each family and the species in each genus are arranged alphabetically. No one book is followed for nomenclature, except that in the grass family Hitchcock's Manual of the Grasses of the United States, 1935, is employed. Other works are listed in the *Literature Cited.*

The sand prairie is here considered a climax to which all other communities are progressing—that "one far-off divine event toward which the whole creation moves"; but even the most optimistic ecologist endowed with the gift of prophecy can hardly see in his mind's eye the craters, troughs, gullies, and rough hills all smoothed out, the streams dried, the low places drained, grazing, plowing, road-building, wind, and torrential rains forever banished. Unless this shall be, the various communities of the sand-hill area may be expected long to remain, some of them as semi-permanent edaphic climaxes. As a matter of fact, even stabilized soil and typical vegetation are subject to degradation. Long spells of dry weather occur with minimum rainfall, as in the years 1930 to 1935; these not only delay the seral changes from Oryzopsis and its associated pioneers to the Stipa-Andropogon-Calamovilfa climax but cause actual reversals. Dry seasons may hasten progress in the hydrarch series, but the areas involved are few and small.

A flora which approaches the mesophytic stage must have, for permanence, a greater rainfall than the plains of Colorado enjoy. Even deficiencies for single seasons are likely to impose difficulties which result in a decrease of individuals of certain species; such reduction of abundance may be or may not be balanced by increases of other species. In any event, the composition and appearance of a given area can not and does not remain identical from year to year. In the years from 1920 to 1928 the sand hills were a "lovely land of flowers"; since then, except in the early spring, they have seemed little more than a desert waste, or in spots perhaps a shadow of their former selves. With the increased rainfall of 1936 and 1937 a slight improvement is shown; this may presage a return to earlier conditions if over-grazing does not continue.

The list of plants given for the sand prairie is typical of the sand areas of northeast central Colorado. In any such study some locally dispersed species are sure to be omitted, and the subjective element in the choice of that which is "typical" can not be avoided. Nevertheless, this list and the lists of the various seral communities (consocies) representing collections made at many times and in at least eight different years, are believed to be fairly

representative. It must also be pointed out that there are "sand hills" having considerable clay; this hard-baking soil does not permit the development of prairie, but supports a "short-grass" cover.

Minor communities, which are numerous, result from variations in physiography, differences in the amount of soil humus, and even "pure chance." Most striking of these, especially in late June, is a stand in which *Stipa comata* so predominates that many of the usual secondary species are excluded or masked. When the Stipa plants ripen their inflorescences, these stand well above the general level of vegetation, and a stretch of this Stipa community looks almost like a field of grain ready for the reaper. Calamovilfa, likewise, forms definite stands, never large—most often from 100 to 10,000 square feet. One such stand observed July 13, 1936 was an almost pure growth of the dominant grass, with occasional plants of *Helianthus petiolaris, Nuttallia stricta,* and *Eriogonum annuum.*

Various societies, most often conspicuous for a few days or perhaps a week, are dominated by flowering herbs, as Abronia, Argemone, Delphinium, Lupinus, Chrysopsis, Chrysothamnus, and Grindelia. *Peritoma serrulatum,* the Colorado bee plant, and *Helianthus petiolaris,* the common sunflower, frequently line trails and roads. *Rhus rydbergii,* the poison ivy of plains and foothills, and *Rhus trilobata,* three-leaved sumac, are the only shrubs which occur in sufficiently close stand to constitute a society, although along dry washes the yellow flowering currant, *Chrysobotrya aurea,* may be represented by small groups of bushes. Local and seasonal societies in this and the other chief plant communities are referred to more fully in a subsequent section of the present paper.

Damage to the association may be brought about in various ways. Autumn or winter grass fires sometimes occur, but fires are not of great extent, since stands of sand prairie are usually of rather small area interspersed among other communities which are either too open or else too wet to burn. Burrowing rodents produce local disturbance of the soil, and permit temporary invasion by annual weeds. Mowing for hay favors the grasses and sedges at the expense of flowering herbs. Grazing, and especially over-grazing, may so reduce the total stand by actual cropping of grasses to the roots and by disturbing the soil through tramping that a retrogression to the open *Muhlenbergia pungens* stage occurs. Such change is most likely to take place during the dry periods of climatic cycles. Studies made by the writer in 1920 showed in overgrazed areas near Roggen, Colorado, a total vegetative cover of from 14 to 28 per cent while the same and similar areas visited again in 1937 ranged from 10 to 20 per cent. At Akron, Colorado, (Savage, 1937) the grass cover of heavily grazed sand soil was only 6.8 per cent.

Records of plot and quadrat studies in various parts of the sand prairie are given in Tables 2 and 3. The relative frequency of a species and the number of species per plot vary greatly; in half of the 0.1-square-meter plots not more than 2 or 3 species occur.

TABLE 2. SAND PRAIRIE (STIPA-ANDROPOGON-CALAMOVILFA)

Study of quadrats with sparse vegetation on somewhat stabilized soil. Quadrat I is 4 meters on a side, quadrats II and III are one meter square. The ground cover is estimated in percentages.

	Quadrat I June 25, 1920	Quadrat II Sept. 12, 1930	Quadrat III Sept. 12, 1930
Bare ground	69	86	74
Stipa comata	11	2	1
Andropogon hallii	9	2	3
Calamovilfa longifolia	2	0	0
Agropyron smithii	1	0	0
Bouteloua gracilis	1	0	0
Muhlenbergia pungens	0	0	4
Cyperus schweinitzii	0	3	2
Eriogonum effusum	0	2	0
Chenopodium oblongifolium	0	1	0
Franseria acanthicarpa	0	1	0
Aster mutiflorus	0	1	1
Helianthus petiolaris	1	1	2
Machaeranthera ramosa	0	1	2
Artemisia filifolia	0	0	5
Yucca glauca	0	0	5
Psoralea lanceolata	1	0	1
Phaca longifolia	1	0	0
Oreocarya suffruticosa	1	0	0
Cirsium plattense	1	0	0
Tradescantia occidentalis	1	0	0
Equisetum kansanum	1	0	0
	100	100	100

TABLE 3. SAND PRAIRIE (STIPA-ANDROPOGON-CALAMOVILFA) NEAR ROGGEN, COLORADO

Frequencies in 50 plots, each 0.1 square meter. The figures show percentages of plots containing each item. (Raunkiaer's hoop method.)

Species list	Series I Aug. 2, 1935	Series II June 17, 1936	Series III June 17, 1936	Series IV July 13, 1936
Stipa comata	0	74	88	86
Calamovilfa longifolia	96	4	38	90
Andropogon hallii	6	8	50	0
Agropyron smithii	0	4	0	32
Oryzopsis hymenoides	0	10	0	0
Muhlenbergia pungens	0	0	6	0
Helianthus petiolaris	84	66	24	6
Equisetum kansanum	0	82	48	0
Chenopodium oblongifolium	74	6	4	0
Psoralea lanceolata	38	0	2	0
Phaca longifolia	0	24	0	0
Gilia polyantha	0	14	0	0
Franseria acanthicarpa	14	0	0	0
Juncus ater	0	4	0	12
Tradescantia occidentalis	0	6	2	6
Nuttallia stricta	4	4	0	0
Abronia elliptica	0	0	4	0
Argemone intermedia	2	0	0	0
Chamaesyce serpens	0	2	0	0
Acrolasia albicaulis	0	2	0	0
Cuscuta indecora	2	0	0	0

Other plants seen near to the plots but not in any of them: *Eriogonum annuum, Salsola pestifer, Melilotus alba, Cirsium plattense.*

Following this account of the Stipa-Andropogon-Calamovilfa sand prairie the various seral communities leading to it will be considered: first the dry series originating on bare upland sand, then the longer array of communities beginning in ponds, ditches, or streams. These, although more numerous than those of the dry series, occupy much less area. Typical sand hills of Colorado support chiefly the *Muhlenbergia pungens* and *Artemisia filifolia* communities.

Loose Sand and Blow-out Community

Dominant and important species:

Oryzopsis hymenoides	*Psoralea lanceolata*
Cristatella jamesii	*Heliotropium convolvulaceum*
Polanisia trachysperma	

Other species:

Muhlenbergia pungens	*Chamaesyce petaloidea*
Redfieldia flexuosa	*Chamaesyce serpens*
Phaca longifolia	*Cirsium plattense*

The members of the loose sand and blow-out community (*Oryzopsis hymenoides* consociation) include only pioneers. In the loose sand carried by wind from blow-outs, Oryzopsis alone at first obtains a foothold, to be followed later by *Psoralea lanceolata.* Oryzopsis, or Indian millet, is a rather tall, early-flowering bunch grass whose roots penetrate far into the sand, while Psoralea is a 10-inch tall legume likewise well-rooted, having small white flowers and nearly spherical pods. *Muhlenbergia pungens* forms dense low bunches, not easily killed by either undermining or by burying with sand.

In the actual blow-out, where vegetation has all been removed but the sand has not become too soft and loose, *Heliotropium convolvulaceum,* a dwarf annual, and the two annual Capparidaceous plants *Cristatella jamesii* and *Polanisia trachysperma* first appear. Resting blow-outs come to have, after a time, the same vegetation as loose sand, and if they are not too much disturbed, their vegetation passes over gradually and very slowly into the *Muhlenbergia pungens* stage, the usual "sand-hills-mixed," an edaphic climax corresponding to the Andropogon bunch grass community of the sand hills of Nebraska.

A very full and interesting account of the formation and growth of blow-outs in the Nebraska sand hills is given by Pool (1914, pages 240-242). His list of pioneer plants is nearly the same as that of the writer, but he finds Redfieldia the first plant to appear in fresh blow-outs. His *Pentstemon haydeni* and *Calamovilfa longifolia* suggest the greater precipitation in Nebraska sand hills. These plants would not be able to establish themselves in blow-out sand of northeastern Colorado. The approximate order of appearance of the earliest 10 species is as indicated in Table 4, but this order varies somewhat in different localities.

TABLE 4. COMPARISONS OF PLANTS OF BLOW-OUTS IN APPROXIMATELY USUAL ORDER OF SUCCESSION IN BARE SAND

Northeastern Colorado:	Nebraska (Pool, 1913):
1. *Heliotropium convolvulaceum*	1. *Redfieldia flexuosa*
2. *Cristatella jamesii*	2. *Psoralea lanceolata*
3. *Polanisia trachysperma*	3. *Cristatella jamesii*
4. *Oryzopsis hymenoides*	4. *Polanisia trachysperma*
5. *Psoralea lanceolata*	5. *Eragrostis trichodes*
6. *Phaca longifolia*	6. *Muhlenbergia pungens*
7. *Chamaesyce petaloidea*	7. *Oryzopsis hymenoides*
8. *Redfieldia flexuosa*	8. *Pentstemon haydeni*
9. *Muhlenbergia pungens*	9. *Munroa squarrosa*
10. *Anogra cinerea*	10. *Calamovilfa longifolia*

In typical "sage sand" of moving dunes, which is described (Savage, 1937) as somewhat more compact than the more usual "Yucca sand," the sand sage, *Artemisia filifolia*, may take the place of the usual pioneer plants of blow-outs. This has been observed by the writer near Brush, Akron, and Otis in northeastern Colorado but especially at Lamar, in southeastern Colorado.

The results of quadrat studies showing different, but perhaps not quite typical, examples of the vegetation of loose sand and blow-outs are recorded in Table 5.

TABLE 5. LOOSE SAND AND BLOW-OUT COMMUNITY *(Oryzopsis hymenoides)*

Quadrat I is 4 meters square, situated on the lee side (east side) of a sand hill in which there is a large blow-out at the west; Quadrat II is of the same size but on level ground near a small reservoir. Both studies were made June 25, 1920. Ground cover is estimated in percentages.

	Quadrat I	Quadrat II
Bare ground	93	92
Oryzopsis hymenoides	1	2
Psoralea lanceolata	3	3
Andropogon hallii	2	0
Petalostemon villosus	1	0
Rumex venosus	0	2
Anogra, Cirsium, Nuttallia	0	1
	100	100

SAND-HILLS-MIXED COMMUNITY

Dominant species:

Muhlenbergia pungens

Important species:

Calamovilfa longifolia
Andropogon hallii
Oryzopsis hymenoides
Tradescantia occidentalis
Eriogonum annuum
Rumex venosus
Lupinus pusillus
Petalostemon villosus
Psoralea lanceolata
Nuttallia stricta
Oreocarya suffruticosa
Franseria acanthocarpa

Erigeron bellidiastrum
Helianthus petiolaris
Othake sphacelata

Frequent species:

Yucca glauca
Acnida tamariscina
Chenopodium oblongifolium
Abronia elliptica
Allionia linearis
Lesquerella argentea
Cristatella jamesii
Polanisia trachysperma
Phaca longifolia
Chamaesyce petaloidea
Chamaesyce serpens
Croton texensis
Rhus rydbergii
Rhus trilobata
Anogra cinerea
Apocynum hypericifolium
Asclepias arenaria
Asclepias speciosa
Gilia longiflora
Lygodesmia juncea
Chrysopsis villosa

Less frequent but usually present species:

Agropyron pauciflorum
Panicum virgatum
Juncus ater
Redfieldia flexuosa
Acrolasia albicaulis
Opuntia fragilis
Opuntia humifusa
Opuntia polyacantha
Anogra nuttallii
Acerates viridifolia
Ipomea leptophylla
Heliotropium convolvulaceum
Physalis longifolia
Pentstemon secundiflorus
Franseria acanthocarpa
Artemisia filifolia
Cirsium plattense
Hymenopappus filifolius
Senecio spartioides

Wide stretches of both rolling and rather abrupt hills in many parts of northeastern Colorado are covered with this "sand-hills-mixed" community in which clumps of *Muhlenbergia pungens* are the characteristic feature. Plants of the dominant species are about 10 inches tall, making matted clumps which form barriers to moving sand and cause the soil to pile up around them. There is never a close stand of Muhlenbergia, the bunches being usually a foot or two apart. Nevertheless they are close enough so that when the plants turn red in autumn the entire landscape shows color, and at a distance the bare ground or the remaining vegetation is scarcely noticed. The composition of this community, as revealed by plot-frequency and quadrat studies, is indicated in Tables 6 and 7. Another study, similar to that recorded in Table 7, was made on the side of an old, not a fresh, blow-out, June 25, 1920. It showed in percentages (for a quadrat 4 meters on a side): bare ground, 83; *Muhlenbergia pungens,* 7; *Psoralea lanceolata,* 4; *Andropogon hallii,* 3; *Sporobolus cryptandrus,* 1; *Phaca longifolia,* 1; *Helianthus petiolaris,* 1.

On hilltops and other exposed places the community has, in addition to the dominant Muhlenbergia, the various species enumerated for the loose sand and blow-out community. Plants of *Yucca glauca* are likely to be frequent, and the tall "evening star," *Nuttallia stricta,* is conspicuous in midsummer. On the lower slopes and more level ground the tall grasses *Andro-*

TABLE 6. SAND-HILLS-MIXED COMMUNITY *(Muhlenbergia pungens)*
FREQUENCY PERCENTAGES IN SERIES OF PLOTS OF 0.1 SQUARE METER

	I	II	III	IV	V
Muhlenbergia pungens	72	80	82	64	12
Helianthus petiolaris	66	62	56	38	24
Psoralea lanceolata	50	48	64	40	40
Oryzopsis hymenoides	16	24	6	8	50
Petalostemon villosus	12	2	0	6	38
Oreocarya suffruticosa	6	0	0	0	0
Nuttallia stricta	6	0	0	4	0
Franseria acanthicarpa	4	10	0	34	8
Peritoma serrulatum	2	0	4	0	4
Andropogon hallii	0	28	0	2	0
Rumex venosus	0	36	0	8	8
Lygodesmia juncea	0	12	0	0	0
Tradescantia occidentalis	0	2	4	6	0
Eriogonum annuum	0	0	2	0	4
Cristatella jamesii	0	0	0	0	12
Heliotropium convolvulaceum	0	0	0	0	2
Machaeranthera ramosa	0	0	0	0	2
Redfieldia flexuosa	0	0	0	2	0
Anogra cinerea	0	0	0	4	0
Physalis longifolia	0	0	0	4	0

NOTE: Columns I, II, III, and V are observations of July 18, 1935; Column IV, August 27, 1935. Each series consists of 50 plots. Series V is in looser soil than the others. This accounts for the presence of Cristatella, and the greater frequency of Oryzopsis, as well as the lesser frequency of Muhlenbergia.

pogon hallii and *Calamovilfa longifolia* appear often in considerable patches. Likewise conspicuous because of their height, and standing well above the Muhlenbergia, are *Eriogonum annuum* and *Helianthus petiolaris;* also noticeable, but rather because of colored inflorescences, are *Petalostemon villosus* with pink spikes of minute flowers, *Erigeron bellidiastrum,* with whitish pink

TABLE 7. SAND-HILLS-MIXED COMMUNITY *(Muhlenbergia pungens)*

A much over-grazed area, the soil with an admixture of clay and humus. Four meter-square quadrats I, II, III, and IV near Orchard, Colorado, September 12, 1930.
Estimated ground-cover percentages:

	I	II	III	IV
Bare ground	74	86	80	85
Artemisia filifolia	5	0	0	0
Yucca glauca	5	0	0	0
Muhlenbergia pungens	4	0	4	3
Andropogon hallii	3	0	0	0
Juncus interior	2	3	3	1
Helianthus petiolaris	2	2	2	1
Aster fluviatilis	2	1	1	1
Aster multiflorus	1	2	1	2
Psoralea lanceolata	1	0	3	1
Chamaesyce serpens	1	0	0	0
Eriogonum effusum	0	2	0	0
Stipa comata	0	2	2	0
Chenopodium album	0	1	0	0
Franseria acanthicarpa	0	1	0	2
Nuttallia stricta	0	0	4	0
Bouteloua gracilis	0	0	0	4

or lavender rays, and *Othake sphacelata,* which is an aster-like plant having reddish-violet rays that are conspicuously tri-lobed.

Hillsides, especially east slopes, sometimes support patches of many square feet or even an acre in extent of the western poison ivy, *Rhus rydbergii,* and sometimes other patches of common dogbane, *Apocynum hypericifolium.* Neither of these species is represented by scattered individuals; the plants grow in rather close contact, although leaving some room for smaller plants, especially grasses, between them.

Plot-frequency studies help an understanding of the composition of the sand-hills-mixed community, and a number of such studies have been made. The western spiderwort, *Tradescantia occidentalis,* is conspicuous in May and early June before much other vegetation develops; hence, with their brilliant blue flowers these plants form a conspicuous feature of the landscape. Using the Raunkiaer hoop method, a series of 1000 plots, each 0.1 square meter, was examined on May 27, 1936 and another series, also of 1000 plots on June 17, 1936. These plots were consecutive, taken in a north-south direction in typical sand hills, not passing through any extensive low area. One might easily guess, because of their conspicuousness, that spiderworts would be recorded in every plot, but they were found in only 16 per cent of the plots of May 27 and in 14 per cent of those examined on June 17. Observations in other localities as far east as the Nebraska and Kansas state lines show about the same frequency of Tradescantia in the spring and early summer flora of rolling sand hills.

The frequency of *Helianthus petiolaris,* so conspicuous in mid- and late summer, was studied in the same way, and the species was found in 56 per cent of the plots. The Helianthus study was made in a part of the sand hills which has been moderately grazed for about 40 years. The sunflower serves somewhat as an indicator of disturbed conditions, being more abundant with heavy grazing and less abundant in more virgin conditions.

SAND-SAGE COMMUNITY

Dominant species:

Artemisia filifolia

Frequent species:

Muhlenbergia pungens | *Sitanion hystrix*
Oryzopsis hymenoides | *Sporobolus cryptandrus*

Other species:

Aristida fendleriana | *Redfieldia flexuosa*
Agropyron inerme | *Stipa comata*
Bouteloua gracilis | *Carex eleocharis*
Buchloe dactyloides | *Yucca glauca*
Festuca octoflora | *Eriogonum annuum*
Hordeum pusillum | *Allionia linearis*
Munroa squarrosa | *Hoffmanseggia jamesii*

Petalostemon villosus	*Monarda pectinata*
Psoralea lanceolata	*Lygodesmia juncea*
Croton texensis	*Franseria acanthocarpa*
Cactus radiosus	*Artemisia frigida*
Opuntia fragilis	*Chrysopsis hirsutissima*
Opuntia humifusa	*Erigeron pumilus*
Nuttallia stricta	*Helianthus petiolaris*
Gilia polyantha	*Hymenopappus tenuifolius*
Phlox depressa	*Senecio riddellii*
Oreocarya suffruticosa	*Sideranthus spinulosus*

Sand sage *(Artemisia filifolia)* and its associates form a semi-permanent community of scattered stands in northeastern Colorado—acres, and sometimes square miles in extent. There is somewhat the appearance of the sage-brush scrub of semi-deserts, but the dominant species is a smaller plant than the desert sage *(Artemisia tridentata)*; it is greener in color, and it occurs only in sandy soils, whereas the desert sage inhabits fine-grained soil. Sand sage flourishes on level or slightly rolling ground where soil is more compact and contains more humus than that which favors *Muhlenbergia pungens*. In places, the sand-sage association includes a considerable number of the species which occur in short-grass communities throughout the high plains. The bushes have a spread of a foot or two, and are widely spaced, with considerable bare ground.

A complete list of plants of the community would repeat most of those in the Muhlenbergia association; but, since compared with the sand sage the grasses here make a poor showing, certain few tall flowering herbs, especially *Eriogonum annuum, Nuttallia stricta, Gilia longiflora, Machaeranthera ramosa,* and, along trails or roads, *Helianthus petiolaris* exert a greater influence on the appearance of the landscape. There is a lack of distinct societies, most species appearing as scattered individuals or small groups, seldom covering any considerable area.

A plot study was made in a typical sand-sage *(Artemisia filifolia)* community between Keensburg and Roggen, Colorado. The sand in this vicinity covers a number of square miles, chiefly on level ground and gentle slopes. It thins out and disappears on hilltops and ridges. Fifty plots were examined, each 15 x 25 feet, and all clumps of sand sage over 10 inches high were counted in each plot. Details of the several plots were tabulated, but are omitted in this paper for lack of space. The average ground area of the clumps was estimated as 2 square feet. In these plots of 375 square feet each, the average number of clumps was 19.3; hence the ground covered by the clumps of sand sage was 38.6 square feet, or about one-tenth of the total area examined, leaving nine-tenths for bare ground, grasses and flowering herbs. The chief grass is grama, *Bouteloua gracilis;* others were noted, especially *Agropyron smithii, Andropogon hallii, Aristida fendleriana, Calamovilfa longifolia, Distichlis stricta, Koeleria cristata, Muhlenbergia pungens, Munroa squarrosa, Oryzopsis hymenoides, Redfieldia flexuosa, Sitanion*

hystrix. Flowering herbs include, among others: *Yucca glauca, Eriogonum effusum, Rumex venosus, Argemone intermedia, Amorpha nana, Psoralea lanceolata, Chamaesyce petaloidea, Chamaesyce serpens, Opuntia humifusa, Nuttallia stricta, Anogra cinerea, Physalis heterophylla, Lygodesmia juncea, Franseria acanthicarpa, Chrysopsis villosa, Gutierrezia sarothrae, Helianthus petiolaris, Hymenopappus tenuifolius, Machaeranthera ramosa.*

The sand-sage community is a more advanced ecological type than the sand-hills-mixed, but stands of the latter may develop into sand prairie (Stipa-Andropogon-Calamovilfa) without passing through the Artemisia stage and without having Artemisia plants at any time. Further, prairie fires and long overgrazing may degrade sand prairie to the sand-sage stage.

South of Brush, Colorado, the overgrazed sand-hills-mixed community of uplands gives way on level ground to sand-sage, and the sand-sage is seen to be working upward. On well-stabilized hills throughout northeastern Colorado the sand-sage community may pass over to upland short grass. Unless protected from fires and overgrazing it does not develop into sand prairie.

Pondweed-Arrowhead Community

Dominant species:

Potamogeton lonchites — *Potamogeton natans*

Sagittaria arifolia

Frequent species:

Alisma plantago	*Lemna minor*
Eleocharis palustris	*Batrachium trichophyllum*
Scirpus americanus	*Ranunculus sceleratus*
Scirpus validus	*Callitriche palustris*

The pondweed-arrowhead association (Potamogeton-Sagittaria) is somewhat feebly represented in temporary ponds and small streams, its development varying within wide limits. A considerable number of species not mentioned in the list actually belong to this aquatic community, but since ponds change much from year to year, while streams among the Colorado sand hills are small, few, and intermittent, there is no great floral richness at any one station. No liverworts and mosses have been collected; if any are present they must be of very local occurrence. The algae which have been examined are chiefly Oscillatoria, Anabaena, Spirogyra, Oedogonium, diatoms, and desmids.

All of the seed plants named as belonging to the community may and do form societies at certain times and places. Since every botanist is familiar with such aquatic vegetation, there is no need for further description.

Cat-tail-Bulrush Swamp

Dominant species:

Scirpus americanus	*Typha latifolia*
Scirpus validus	*Eleocharis palustris*

Other species:

Spartina gracilis	*Rumex mexicanus*
Carex lanuginosa	*Bidens glaucescens*
Carex nebraskensis	*Bidens vulgata*
Eleocharis acicularis	

The cat-tail-bulrush association (Typha-Eleocharis-Scirpus) exists as restricted areas of level swampland either in the center of depressions, or "sinks," or as interrupted patches flanking the course of streams. Just as aquatic habitats are few in the Colorado sand hills, so also are swamps. Where present, they all exhibit great similarity. Species tend to mass their individuals in societies. Stands are close, and hence few plants from other communities are able to enter. It is only when the water is highly alkaline or in situations which vary greatly in soil-water content from time to time through the growing season that there is any open ground. Even then other plants do not come in to any extent—either the soil is too soggy, that is, lacking in drainage, or it may be dry at critical periods, or it is well occupied with a dense growth of interlacing roots and rhizomes. Further, the usual alkalinity of lowland soil water restricts the establishment of many species.

A piece of swamp or marsh which may be considered as belonging to this association, although on the way toward meadow conditions, was examined on June 17, 1936, and found to be made up chiefly of *Scirpus americanus.* Subordinate plants, in approximate order of importance, are: *Hordeum jubatum, Melilotus alba, Rumex mexicanus, Poa interior, Andropogon hallii, Carex praegracilis, Distichlis stricta, Scirpus validus, Salix amygdaloides* (seedlings). Another stand of this community, but well on the way to the grass meadow stage, was studied July 18, 1935 for frequency of species by the Raunkiaer hoop method (50 plots, each 0.1 square meter). The various species occurred in the plots in the following percentages: *Scirpus americanus,* 52; *Agropyron smithii,* 42; *Juncus ater,* 30; *Aster exiguus,* 30; *Carex sterilis,* 22; *Juncus torreyi,* 18; *Panicum virgatum,* 10; *Carex nebraskensis,* 8; *Koeleria cristata,* 6; *Helianthus petiolaris,* 2.

MOIST STREAMBANK COMMUNITY

Dominant species:

Equisetum kansanum	*Berula erecta*

Mentha penardi

Important species:

Agrostis alba	*Puccinellia nuttalliana*
Agrostis hyemalis	*Spartina gracilis*
Muhlenbergia asperifolia	*Carex lanuginosa*

Other species:

Persicaria omissa	*Epilobium lineare*
Halerpestes cymbalaria	*Sium cicutarium*
Epilobium adenocaulon	*Lycopus americanus*

Lycopus lucidus	*Bidens glaucescens*
Teucrium occidentale	*Bidens vulgata*
Gerardia besseyana	*Gnaphalium macounii*
Mimulus geyeri	*Gnaphalium proximum*
Lactuca pulchella	

The moist streambank community (Equisetum-Berula-Mentha) occurs as a narrow strip along the edges of ditches and slow-running streams where drainage is better than in swamp and marsh land. When a stream changes its course and forsakes an area of this community a grass meadow develops—Agropyron-Hordeum-Panicum—without passing through a sedge and rush stage.

Because of the abundance of water the stand is close, leaving no bare ground. There is a tendency to produce societies, especially with *Equisetum kansanum, Puccinellia nuttalliana, Spartina gracilis,* and *Halerpestes cymbalaria.* The species of *Agrostis* and also *Muhlenbergia asperifolia* are widely scattered through the drier parts of any stand of this community. Incidentally it may be remarked that *Muhlenbergia asperifolia* is not happily named; it is much less "asperifolious" than *Muhlenbergia pungens* of upland sand.

SEDGE-RUSH MARSHLAND

Dominant species:

Carex lanuginosa	*Juncus ater*
Carex nebraskensis	*Juncus torreyi*

Other species:

Agropyron smithii	*Juncus interior*
Agrostis alba	*Juncus vallicola*
Alopecurus aristulatus	*Iris missouriensis*
Distichlis stricta	*Sisyrinchium angustifolium*
Muhlenbergia asperifolia	*Persicaria pennsylvanica*
Poa interior	*Halerpestes cymbalaria*
Carex praegracilis	*Eustoma russellianum*
Carex sterilis	*Gerardia besseyana*
Cyperus acuminatus	*Crepis perplexans*
Eleocharis palustris	

Besides the species listed there are scattered individuals of species belonging rather to meadow and to sand prairie.

The sedge-rush marshland (Carex-Juncus) is especially conspicuous in early spring because of the dark inflorescences of *Carex nebraskensis* and *Juncus ater,* the former in the wetter situations, the latter in drier places. Other species of Carex and Juncus are less noticeable but help to make up a considerable part of the community.

With building up of the ground or lowering of water-table the sedges and rushes tend to become replaced by grasses and flowering herbs; *Carex praegracilis* and *Juncus ater* are, however, very persistent, remaining often as considerable patches after most of the sedges and rushes have been crowded out, and a mixed meadow has developed.

Salt grass, *Distichlis stricta*, often makes patches of greensward in depressions, and since it is apparently not palatable to stock is likely to remain or even increase where there is considerable grazing. The few species of flowering herbs are represented by a small number of individuals. The various sedges and rushes tend to form alternating societies within the community. There is no bare ground.

A stand of this community was studied by the Raunkiaer hoop method on June 17, 1936. In this stand *Scirpus americanus*, reminiscent of the Typha-Eleocharis-Scirpus stage, was abundant throughout, while *Carex nebraskensis* and *Carex lanuginosa* were infrequent, an indication that the marsh is drying, thus proceeding to the meadow stage. Frequency percentages were recorded: *Scirpus americanus*, 86; *Carex praegracilis*, 68; *Poa interior*, 64; *Hordeum jubatum*, 62; *Aster fluviatilis*, 40; *Juncus ater*, 26; *Melilotus alba*, 16; *Agropyron smithii*, 8; *Carex nebraskensis*, 6; *Carex lanuginosa*, 6; *Helianthus petiolaris*, 2.

Another stand of sedge-rush marshland examined July 13, 1936 consists of the following species, the most abundant named first and the others in order: *Scirpus americanus, Carex praegracilis, Juncus ater, Agropyron smithii, Poa interior, Andropogon hallii, Carex nebraskensis, Juncus torreyi.* This is a very dense growth—practically closed. The only flowering herb recognized is an Epilobium.

Carex praegracilis and *Poa interior* show a high degree of fidelity throughout this type of marshland, often being well-nigh uniformly distributed, yet they are never in sufficient abundance to be rated as dominant or even sub-dominant. In moister parts, *Scirpus americanus* reaches 100 per cent frequency and forms a large part of the total ground cover. In drier locations *Juncus ater* increases and the Scirpus decreases.

WILLOW-POPLAR COMMUNITY

Dominant Species:

Populus sargentii	*Salix amygdaloides*

Other species:

Equisetum kansanum	*Chenopodium oblongifolium*
Equisetum variegatum	*Chrysobotrya aurea*
Agropyron pauciflorum	*Roripa sinuata*
Agropyron pseudorepens	*Eustoma russellianum*
Elymus canadensis	*Verbena hastata*
Hordeum jubatum	*Solanum nigrum*
Juncus ater	*Lactuca ludoviciana*
Allium textile	*Aster fluviatilis*
Salix exigua	*Lactuca pulchella*
Persicaria omissa	*Solidago canadensis*

Additional species belong properly to the next preceding and succeeding stages of succession.

The willow-poplar community (Salix-Populus) appears as small and isolated stands in depressions among the sand hills or, very rarely, along gulches and sand draws. Only a few trees occur together, most often three or four. There are not many shade plants because of the openness of the community. It might be expected that Smilacina, Thalictrum, Thermopsis, Heracleum, Washingtonia, and Galium would be present, but they do not appear in collections made by the writer. The golden currant, *Chrysobotrya (Ribes) aurea,* sometimes wanders away from the willows and poplars, and extends in small numbers along steep slopes. The endurance of stands of the willow-poplar community depends on the relative permanence of the necessary physiographic features. As steep banks assume a more gentle slope, hills become flattened out, and depressions are filled; trees and shrubs will disappear to give place to grasses and flowering herbs of the Stipa-Andropogon-Calamovilfa sand prairie.

GRASS MEADOW

Dominant species:

Agropyron pauciflorum
Agropyron pseudorepens
Agropyron smithii
Hordeum jubatum
Panicum virgatum

Important species:

Elymus canadensis
Poa interior
Poa pratensis
Spartina gracilis
Carex praegracilis

Other species:

Equisetum kansanum
Agropyron inerme
Agrostis alba
Sphenopholis obtusata
Carex sterilis
Cyperus schweinitzii
Juncus ater
Juncus interior
Juncus torreyi
Tradescantia occidentalis
Sisyrinchium occidentale
Chenopodium oblongifolium
Verbena hastata
Scutellaria brittonii
Physalis heterophylla
Gerardia besseyana
Linaria canadensis
Crepis perplexans
Lactuca pulchella
Aster multiflorus
Aster fluviatilis
Grindelia erecta
Helianthus petiolaris
Othake sphacelata
Solidago canadensis

The grass meadow (Agropyron-Hordeum-Panicum) is an edaphic subclimax which occupies level areas of valley floors; because of its luxuriance it supplies most of the native hay of sand-hill districts. The grasses spread by means of rhizomes, and form a tough sod which prospective invaders do not easily penetrate. This is essentially a closed community with rather few species, the individuals of these often massed in societies. The sandy soil has considerable humus near the surface, resulting from the decay of the abundant vegetation.

If every year had as much precipitation as the wettest ones, this community would form a permanent climax, but during the recent years of drought (1930-1935) the water level in the sand hills has dropped so much that the yield of hay has been reduced, and species with lower water requirement have been favored. It is evident that geographic and climatic influences are tending to produce drier soil conditions with the consequent invasion by more xeric grass species than *Hordeum jubatum* and *Panicum virgatum*—especially Koeleria, Stipa, *Sporobolus crytandrus,* Calamovilfa, Sitanion, and Aristida—thus converting the community into the rather stable mixed semi-xerophytic grassland of level areas through the sand-hill region, denominated in this paper the sand prairie or Stipa-Andropogon-Calamovilfa association.

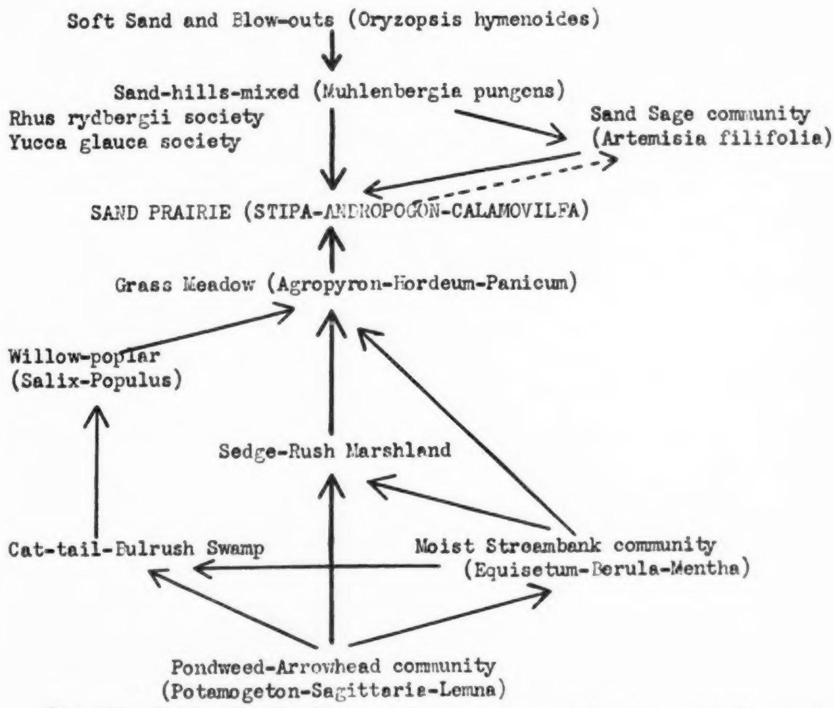

FIG. 10. Successional relations of plant communities in sand-hills areas of northeastern Colorado.

SUCCESSION

Succession in the sand-hills area has been referred to briefly in the descriptions of the various plant communities. The ultimate vegetation of sandy soil which does not become compact and hard is a grassland of tall and medium-height grasses with conspicuous flowering herbs—what is called in this paper the sand prairie or Stipa-Andropogon-Calamovilfa Association, being the western equivalent of the tall-grass prairie of Illinois, Minnesota, and Iowa. This prairie is reached by a series of stages starting either in loose sand or in the water of ponds or streams of sand-hill areas. The several steps are indicated in the chart, Fig. 10, which shows the genetic relations

of the various communities. When sand prairie is plowed for crops and later abandoned it grows up first to a miscellaneous assortment of ruderals, and these become slowly displaced after many years so that a variety of sand-hills-mixed vegetation comes into existence. With sufficient time and if the land is not over-grazed it may be expected to return to prairie.

As indicated previously, and as shown in Fig. 10, successional stages may be skipped in certain localities, especially in the hydrosere, and at times there are likely to be reversals because of long periods of drought or other climatic or even local influence.

DEPRESSIONS OR SINKS

Scattered through sand-hill areas certain undrained depressions exist, some of them so deep that they reach the water-table and hold standing water, especially in the spring and early summer. The deeper sinks have a clump of *Typha latifolia* or *Scirpus validus* in the center, surrounded by a series of circum-areas with less and less soil-moisture and hence supporting more xeric plants. The drier sinks lack Typha and the tall Scirpus, and often have in their central area a stand of Carex or of *Panicum virgatum* or of goldenrod, *Solidago canadensis.* If the central area contains Carex there may be one or two cottonwood trees or peach-leaved willows among the sedges.

The bottom of a depression is often very gently sloping toward the center; in such cases the circum-areas are ill-defined, and there may be stretches of a few hundred feet chiefly of Solidago dotted with small islands of *Rhus rydbergii, Asclepias speciosa,* or *Panicum virgatum.* Stands of the Solidago society are dense, as a rule, permitting little invasion of other flowering herbs or of grasses. Sinks have an alkaline soil, the pH about 9.0 toward the center; hence species are few in number.

The vegetation of two typical sinks is indicated in the following tabulation. Each has four circum-areas (b,c,d,e) surrounding a central area (a). They have the following more abundant species:

I	II
a. *Typha latifolia*	a. *Scirpus validus*
	Scirpus americanus
b. *Carex* spp.	b. *Solidago canadensis*
Juncus torreyi	c. *Agropyron smithii*
Salix amygdaloides	*Agrostis alba*
c. *Panicum virgatum*	*Andropogon hallii*
Juncus ater	*Hordeum jubatum*
Solidago canadensis	*Poa pratensis*
d. *Andropogon hallii*	d. *Calamovilfa longifolia*
Elymus canadensis	*Stipa comata*
Glycyrrhiza lepidota	e. Sand-hills-mixed community
Othake sphacelata	
e. Sand-hills-mixed community	

The circum-areas outside of the central area may be two or more; they most often include the following plants named from the inside of the area outward: *Panicum virgatum, Solidago canadensis, Muhlenbergia asperifolia, Hordeum jubatum, Calamovilfa longifolia, Juncus ater, Elymus canadensis, Andropogon hallii, Sphenopholis obtusata, Stipa comata.* Usually two or more species will form a circum-area, the plants somewhat mixed or in alternating patches. At the outer margin of the sink there may be an interrupted ring of some of the more mesophytic constituents of the upland sand hill flora, as *Othake sphacelata* and *Apocynum hypericifolium.*

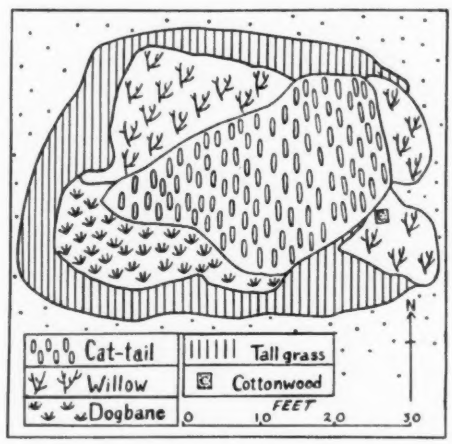

FIG. 11. Cat-tail Sink A, among sand hills near Roggen, Colorado, August 6, 1930. Cat-tails in the center are followed by willows and dogbane, and these surrounded by a zone of tall grasses. Outside of the sink there is typical upland sand-hills vegetation (sand-hills-mixed).

"Cat-tail Sink A," a depression which was mapped on August 19, 1936 (Fig. 11), has a central area of cat-tails which is surrounded for about two-thirds of its circumference by low willows *(Salix exigua)* and the other one-third by dogbane *(Apocynum hypericifolium).* Outside of this circum-area there is a zone of tall grasses around the north, west and south, while at the east this tall-grass zone is so narrow as to be almost indistinguishable, the willow scrub giving way rather abruptly to typical upland sand-hill vegetation dominated by *Muhlenbergia pungens.* The cat-tails, willows, and dogbane form close stands with very little undergrowth. Plants of the tall-grass zone are *Andropogon hallii, Panicum virgatum,* and *Stipa comata,* with goldenrod *(Solidago canadensis)* at the inner margin.

A depression which may be called "Cat-tail Sink B" (Fig. 12) was mapped on August 29, 1930; it shows five rather clearly defined areas: (1) central area of cat-tails; (2) circum-area of sedgeland, chiefly *Carex nebraskensis,* with some scattered peach willows, *Salix amygdaloides;* (3)

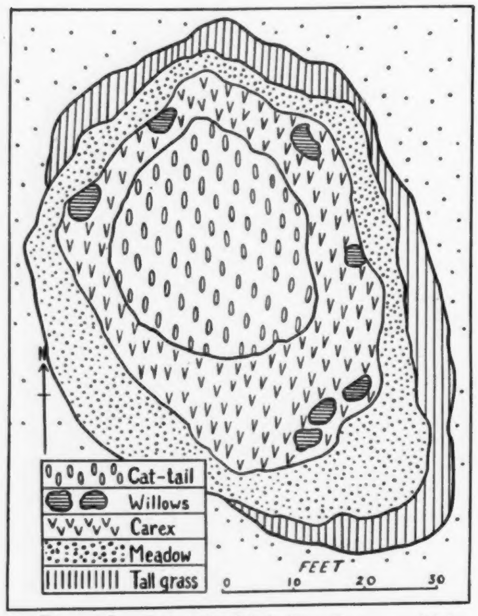

FIG. 12. Cat-tail Sink B. From within out: cat-tails, Carex with willow clumps, mixed meadow, tall grasses; then the usual sand-hills-mixed.

mixed meadow of *Elymus canadensis, Hordeum jubatum, Muhlenbergia asperifolia, Panicum virgatum, Spartina gracilis, Sporobolus cryptandrus, Carex praegracilis, Juncus torreyi, Melilotus alba, Epilobium adenocaulon, Lycopus americanus, Mentha penardi, Lactuca pulchella, Solidago canaden-*

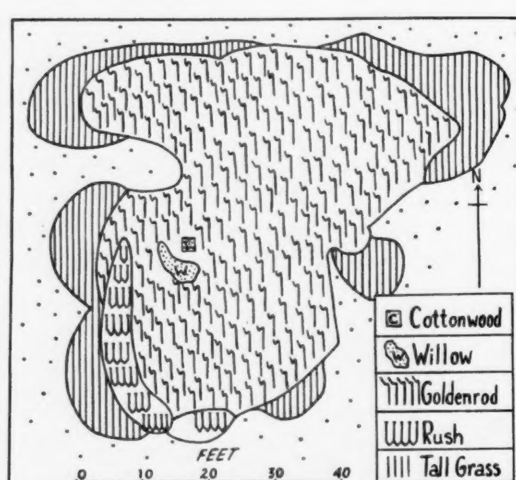

FIG. 13. Goldenrod Sink. This is a sink which has passed the marsh stage, and the vegetation is now mesophytic. The goldenrods will soon be replaced by grasses and other plants of the sand prairie (Stipa-Andropogon-Calamovilfa).

sis; (4) circum-area of tall grasses, including *Andropogon hallii, Calamovilfa longifolia, Sphenopholis obtusata,* with an infiltration of the more mesic flowering herbs of the upland sand-hills vegetation; (5) sand-hills-mixed community.

"Goldenrod Sink" is older and drier than either of the two cat-tail sinks. This was mapped on August 6, 1931 (Fig. 13). The central area is taken up largely with *Solidago canadensis* through which is scattered *Elymus canadensis* and some large clumps of *Panicum virgatum,* as much as 2 or 3 meters in diameter. There is one cottonwood tree and a small willow thicket *(Salix amygdaloides).* An interrupted ring of crescent-shaped clumps of tall grass surrounds the central area; between the crescents the typical upland sand-hill vegetation meets abruptly the sand prairie grassland. At one part in the southwest portion of the sink a large crescent of *Juncus ater* occurs just centralward of one of the tall grass crescents. It is evident that the central area will become at no distant time a stand of sand prairie, the Stipa-Andropogon-Calamovilfa association.

STABILIZED HILLS HAVING STEEP SLOPES AND DRAWS

Old and well-established hills have a flora somewhat different from that of the looser sand which is chiefly considered in this paper. The short grasses, Bouteloua and Buchloe, are present just as in ordinary upland areas of the plains region. The compactness of the soil permits steep slopes in draws and gulches, with an opportunity for the growth of a few shrubs and even small trees in protected sites. The soil is essentially fine-grained; run-off is considerable, hence rather xeric conditions prevail on upper slopes, whereas there is considerable moisture in gulch bottoms. In the loose sand of typical sand hills on the contrary any precipitation sinks in where it falls, so that deep-rooted grasses and flowering herbs make up most of the flora.

The frequent and conspicuous species of these stabilized hills are named in the following lists. In each list the plants are arranged in taxonomic sequence as to family, but alphabetically by genera and species in each family.

a. Dominant species, but often replaced or masked: *Bouteloua gracilis, Buchloe dactyloides.*

b. Frequent species: *Agropyron dasystachyum, Andropogon scoparius, Aristida fendleriana, Koeleria cristata, Munroa squarrosa, Sitanion hystrix, Allium textile, Eriogonum effusum, Lesquerella argentea, Glycyrrhiza lepidota, Orophaca tridactylica, Petalostemon oligophyllus, Psoralea tenuifolia, Croton texensis, Tithymalus robustus, Sphaeralcea coccinea, Cactus radiosus, Opuntia fragilis, Anogra nuttallii, Gaura coccinea, Meriolix serrulata, Phlox depressa, Lithospermum canescens, Plantago purshii, Artemisia frigida, Chrysopsis villosa, Sideranthus spinulosus.*

c. Woody plants, occasional in draws and on slopes: *Celtis reticulata, Atriplex canescens, Chrysobotrya aurea, Ribes inebrians, Amelanchier alni-*

folia, Rosa fendleri, Prunus melanocarpa, Rhus cismontana, Rhus trilobata, Symphoricarpos symphoricarpos.

In general, the stabilized sand hills of Colorado show in their vegetation a resemblance to mixed prairie, described so well by Albertson (1937) for west central Kansas, yet they are almost as near to the true prairie of eastern Nebraska. The soil of even well stabilized sand hills is not so hard and impervious as that in mixed prairie areas, and this looseness of soil is more favorable to deep-rooted prairie plants.

RUDERALS

A comparatively small number of ruderal plants occurs in the sand-hills area. Those most characteristic of roadsides and waste ground are the following, which are listed in the systematic order of Engler and Prantl, except that genera and species in a family are arranged alphabetically. Introduced species are marked with an asterisk (*).

Agropyron smithii
**Agrostis alba*
Agrostis hyemalis
Cenchrus pauciflorus
**Hordeum jubatum*
Panicum capillare
**Poa pratensis*
**Polypogon monspeliensis*
**Syntherisma sanguinale*
**Chenopodium album*
Cycloloma atriplicifolium
**Salsola pestifer*
Acnida tamariscina
**Chorispora tenella*
Lepidium densiflorum
**Norta altissima*
Peritoma serrulatum
**Tribulus terrestris*
Glycyrrhiza lepidota
**Melilotus alba*
**Melilotus officinalis*
**Solanum nigrum*
Ambrosia elatior
Iva xanthifolia
Grindelia erecta
Helianthus petiolaris

A study of ruderals in eastern Colorado made by Shantz (1917) deals chiefly with areas of hard-baking soils, hence his plants are different from these here listed. Only two of the species of sand-hill roads and waste places, *Chenopodium album* and *Salsola pestifer*, are named in Shantz's account.

LOCAL AND SEASONAL SOCIETIES

In the foregoing account of communities some mention is made of species which form local societies, that is, patches or limited areas in which certain usually subordinate species have such high frequency or abundance that they attract attention either throughout the growing period or merely at a particular season. Such minor communities are likely to be conspicuous wherever stands are open and species are few. A brief enumeration of these societies within the major communities follows:

Soft sand and blow-outs.—*Psoralea lanceolata* forms local societies.

Sand-hills-mixed.—Local and seasonal societies are formed by: *Yucca glauca, Psoralea lanceolata, Rhus rydbergii, Rhus trilobata.* The species of Rhus do not lead here to thicket as in dunes of Presque Isle, Pennsylvania

(Jennings, 1909) or San Francisco (Ramaley, 1918). Other societies are those of *Ipomoea leptophylla, Apocynum hypericifolium, Helianthus petiolaris.* Early in the growing season *Tradescantia occidentalis* is conspicuous, but the plants are scattered; during August and early September great numbers of plants of *Nuttallia stricta* are in bloom, giving a white aspect to the community; these plants likewise are not aggregated into definite patches, being rather evenly dispersed.

Sand-sage community.—The chief local societies are of *Bouteloua gracilis, Carex eleocharis, Plantago purshii, Artemisia frigida,* and *Helianthus petiolaris.*

Sand prairie.—In this community the following may be locally massed in such numbers as to constitute recognizable societies: Andropogon, Calamovilfa, Stipa, Abronia, Argemone, Delphinium, Chrysobotrya, Lupinus, Peritoma, *Rhus rydbergii, Rhus trilobata,* Gilia, Apocynum, Physalis, Chrysothamnus, Grindelia, Helianthus.

Grass meadow.—Species of the following genera form local or seasonal societies: Agropyron, Hordeum, Panicum, Carex, Juncus, Peritoma, Physalis, Crepis, Helianthus, and Solidago.

Sedge-rush marshland.—In this community species of Distichlis, Carex, and Juncus form societies which are clearly discernible throughout the growing season.

Willow-poplar community.—Salix (shrubby species), Equisetum, *Hordeum jubatum, Juncus ater,* and *Solidago canadensis* may be sufficiently massed to constitute local societies.

Moist stream-bank community (Equisetum-Berula-Mentha).—Equisetum, Puccinellia, Spartina, Halerpestes, and Bidens may form minor societies. Reproduction by rhizomes is the rule here, as among other communities in sandy soil, so that many species produce patches or even extensive stands.

Cat-tail-bulrush swamp.—All dominant and frequent species have the social habit.

Pondweed-arrowhead community.—All the dominant and frequent species of this community have the social habit.

The local societies just listed depend for their sociability chiefly on vegetative reproduction; a few, however, are annuals and are massed in numbers because the seeds are dispersed locally in quantity, not evenly spread over wide areas. Aside from introduced weeds, the most common annuals forming societies in the sand-hill region are the Colorado bee plant and the sunflower *(Peritoma serrulatum* and *Helianthus petiolaris).*

Besides the societies of local occurrence there are, in the drier parts, certain rather uniformly-spread species, not truly social, which may occur in sufficient numbers to be conspicuous features of the landscape in some locations and at certain seasons, although in other places they appear only as scattered individuals. Most striking of these are: *Rumex venosus* in May

and early June, bearing large-winged pink fruits; *Petalostemon villosus* in mid- and late July with pink, catkin-like spikes, abundant enough to produce a pinkish landscape; *Erigeron bellidiastrum* with heads having lavender rays, a feature of late July and August; *Othake sphacelata*, chiefly about September 1, bearing flower-heads whose pinkish-purple rays give color to the dry landscape of the sand hills just as *Petalostemon villosus* did a month earlier. And while color in the landscape is under consideration, the red of mid- and late September due to autumn coloration of the leaves and stems of *Muhlenbergia pungens* must not be omitted. The bursts of color in the dry sand hills due to Petalostemon, Othake, and Muhlenbergia come after a between-seasons period of comparative dullness, as in early July, when there are almost no flowers. Yet, throughout the estival and serotinal periods there are a few of the following plants in flower, although perhaps so few that they make no impression on the landscape: *Eriogonum annuum, Allionia linearis, Cristatella jamesii, Asclepias speciosa, Gilia longiflora, Heliotropium convolvulaceum* and, in disturbed soil, *Peritoma serrulatum* and *Helianthus petiolaris.*

THE SEASONAL MARCH OF VEGETATION

Prevernal aspect.—By the middle of May although there is little fresh vegetation on uplands, and the grasses are not started, yet *Rumex venosus* plants are already in bloom on lower slopes of the sand hills; *Oreocarya fruticosa* is coming into blossom, widely scattered on hills and rolling ground; some new shoots are appearing on *Rhus rydbergii, Psoralea lanceolata,* and *Apocynum hypericifolium; Juncus ater* stands are now conspicuous, the plants in bud and blossom; *Carex nebraskensis* has reached its full height and now shows its dark brown, almost black, inflorescences. In the sand prairie (Stipa community) there are enough of the following to be conspicuous even at a little distance: spiderwort *(Tradescantia occidentalis),* sand verbena *(Abronia fragrans),* bladder pod *(Lesquerella argentea).* Much less abundant, and so small as to be inconspicuous, are the plants of *Acrolasia albicaulis.* Some white evening primroses *(Anogra cinerea)* are now in bloom, widely scattered over the sand hills.

Vernal aspect.—In late May and early June the appearance of the sand-hill area differs considerably in different years, depending on moisture and temperature. It may be that there are few flowers at this time. Indian millet (Oryzopsis) is now a few inches tall and has a few stray plants in blossom, but all are growing rapidly and soon to be in fruit; *Psoralea lanceolata* is nearly of full height but has no flowers as yet; white evening primroses may be few or many; white-flowered thistles are blooming on hillsides, much scattered, not forming societies; yuccas are starting to bloom; the prickly poppy (Argemone) is in bud. In favorable seasons this is the blue and white period: Tradescantia blue and Anogra white in looser soil, while in somewhat stabilized ground blue larkspurs and white Argemone and the white

sand verbena (Abronia) are conspicuous. *Phaca longifolia* is nearly through blossoming, but its mottled bladdery pods are still seen. Dogbane is not yet in full flower but shows greenish-white buds. *Rumex venosus* is now in fruit, and the plants are drying up; the large-flowered morning glory *(Ipomoea leptophylla)* is in bloom; sunflower seedlings are abundant; species of Phlox occur in more stabilized soil. In rather mesic areas *Stipa comata* has awns almost full length; tansy mustard (Sophia) and spiderwort are widely scattered, while *Allium textile* is locally frequent. In still lower, wetter, and better stabilized ground Juncus and Carex are conspicuous. Present with the sedges and rushes are *Halerpestes cymballaria, Sisyrinchium angustifolium,* and *Ranunculus abortivus*, in small numbers. In sinks and wet places cat-tails are half-grown. Toward the end of June in stable grassland of sand prairie the porcupine grass (Stipa) is very prominent; the Opuntias are about through flowering; dogbane is nearly at the height of its blooming period. On the whole, the end of June shows rather few species in flower.

Estival aspect.—In early July, although this may be called a "between season" time, *Psoralea lanceolata* is in blossom and common everywhere in upland areas; a few sunflowers are now blooming, and also *Chenopodium oblongifolium; Allionia linearis* is conspicuous where present but is much scattered. Cuscuta, frequent on Psoralea, is budding. The annuals *Cristatella jamesii* and *Heliotropium convolculaceum* are far apart yet conspicuous in blow-outs where without them, the soil would be quite bare. A few of the summer grasses are starting to bloom, but most of them are not full-grown; *Eriogonum annuum,* now half its full height, shows some white in its young inflorescence; *Nuttallia stricta,* which will be so conspicuous a little later, is budding; *Argemone intermedia* is in bloom, showing a few scattered societies; Tradescantia, so prominent in spring, is now hard to find; only the dry plants are left.

Toward the end of July, which marks the close of the estival period, the conspicuous plant of upland sand is a hairy, pink-flowered prairie-clover, *Petalostemon villosus*. Indeed this plant so dominates the sand hills that this time may be called the "prairie-clover period." Summer-blooming grasses have reached their prime, and the short-day sunflower *(Helianthus petiolaris)* and Colorado bee plant *(Peritoma serrulatum)* are becoming a recognized part of the landscape.

Serotinal-Autumnal aspects.—Mid-August is, in most years, the time of greatest flower abundance. Prairie clover and Colorado bee plant continue with their pink coloration. Upland sand areas show many plants of the white evening-star *(Nuttallia stricta)* and the aster-like pink-flowered *Othake sphacelata,* while *Gilia longiflora* and *Eriogonum annuum* are abundant on level ground. The low-growing Heliotropium continues in blow-outs and loose sand. Sunflowers are scattered throughout, except in sinks and lowland areas.

About September 1 in certain years *Muhlenbergia pungens* turns so red as to impart a crimson color to the whole landscape; in other years these grasses are so overtopped with evening star and sunflower that they are hardly noticed. Tansy aster, *Machaeranthera ramosa,* is another tall plant of this period. The goldenrod in the central area of sinks blooms late in August and is dry and withered by September 30. Indeed, after that date only a few sunflowers, tansy asters, and evening-stars are left, save along ditches where water-plantain, arrowhead, and Bidens may continue for another week or two.

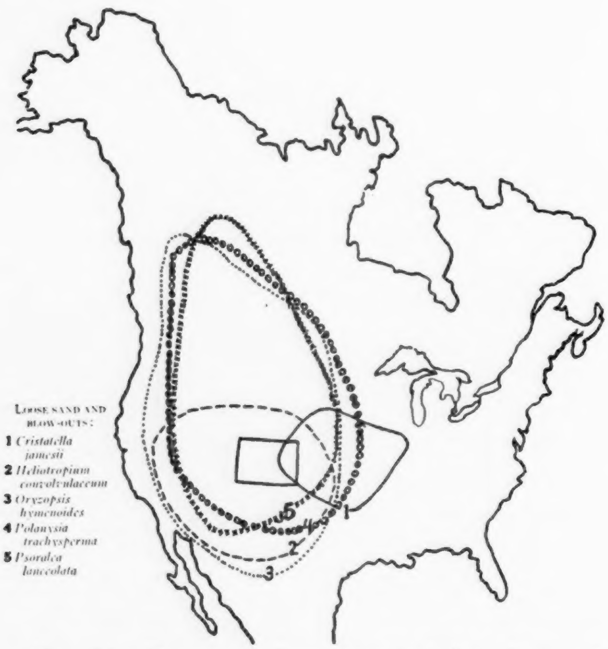

FIG. 14. Ranges of five characteristics plants of loose sand and blow-outs.

GEOGRAPHIC RELATIONS OF THE SAND-HILLS FLORA

To study the geographic relations of the sand-hills flora eight ecological groups of plants have been made, and for each group the distribution has been mapped of the half-dozen or so most characteristic species. Ranges for grasses have been taken from Hitchcock (1935) and for other plants from Rydberg (1917, 1932). The list of groups follows, with genus names alphabetically arranged.

1. *Upland plants characteristic of loose sand and blow-outs: Cristatella jamesii, Heliotropium convolvulaceum, Oryzopsis hymenoides, Polanysia trachysperma, Psoralea lanceolata* (Fig. 14). Most of the species of this group extend in every direction beyond the limits of Colorado for 500 to 1,000 miles, so that for them Colorado is at about the center of their area of distribution; but one of the species, *Cristatella jamesii,* has its range to

the east with its distributional center near the northeast corner of the state of Nebraska.

2. *Upland flowering herbs of early spring: Abronia fragrans, Anogra cinerea, Oreocarya suffruticosa, Rumex venosus, Tradescantia occidentalis*

FIG. 15. Ranges of five characteristic flowering herbs of upland sand areas.

FIG. 16. Ranges of six characteristic grasses of upland sand areas.

(Fig. 15). These plants do not range so widely as the species of our first group, and two of them do not pass west of the Rocky Mountains.

3. *Upland grasses: Andropogon hallii, Calamovilfa longifolia, Muhlenbergia pungens, Oryzopsis hymenoides, Redfieldia flexuosa, Stipa comata* (Fig. 16). In this group all of the species cross the Rocky Mountains, and Colorado is roughly the geographical center of all except *Calamovilfa longifolia* which ranges north, west, and east but does not extend south of the Colorado sand hills.

FIG. 17. Ranges of six characteristic summer-flowering herbs of upland sand areas.

4. *Upland flowering herbs of summer: Gilia longiflora, Helianthus petiolaris, Nuttallia stricta, Othake sphacelata, Petalostemon villosus, Psoralea lanceolata* (Fig. 17). The geographic range of these species is wide, and all cross over the Rocky Mountains except *Othake sphacelata*. The range of this species is chiefly to the south, extending some distance into Mexico.

5. *Upland late-blooming flowering herbs: Artemisia filifolia, Eriogonum annuum, Franseria acanthocarpa, Machaeranthera ramosa, Othake sphacelata, Peritoma serrulatum* (Fig. 18). These species also have wide ranges except *Machaeranthera ramosa* which does not pass the Rocky Mountains to the west and which extends only some 300 miles to the east and north of the Colorado sand hills. *Othake sphacelata*, already mentioned in the previous group—for it may be classified as both summer- and late-blooming—likewise is limited westward by the mountains.

6. *Lowland grasses: Agropyron pauciflorum, Agropyron smithii, Hor-*

FIG. 18. Ranges of six characteristic late-blooming herbs of upland sand areas.

FIG. 19. Ranges of five typical grasses of lowland stations in the sand-hills area. The wide distribution of these lowland species is in contrast to the more limited distribution areas of upland grasses shown in Fig. 16.

deum jubatum, Panicum virgatum, Poa interior (Fig. 19). Plants of this group all have wide distribution, some extending across the continent from east to west and ranging from far north well into Mexico. All cross the Rocky Mountains and go far beyond the western boundary of Colorado.

7. *Lowland sedges and rushes: Carex nebraskensis, Carex praegracilis, Eleocharis palustris, Juncus ater, Juncus torreyi, Scirpus americanus* (Fig. 20). These plants show distributions much like those of the lowland grasses; all pass the Rocky Mountains and go as far west as California, and all go out of Colorado to the north, east, and south.

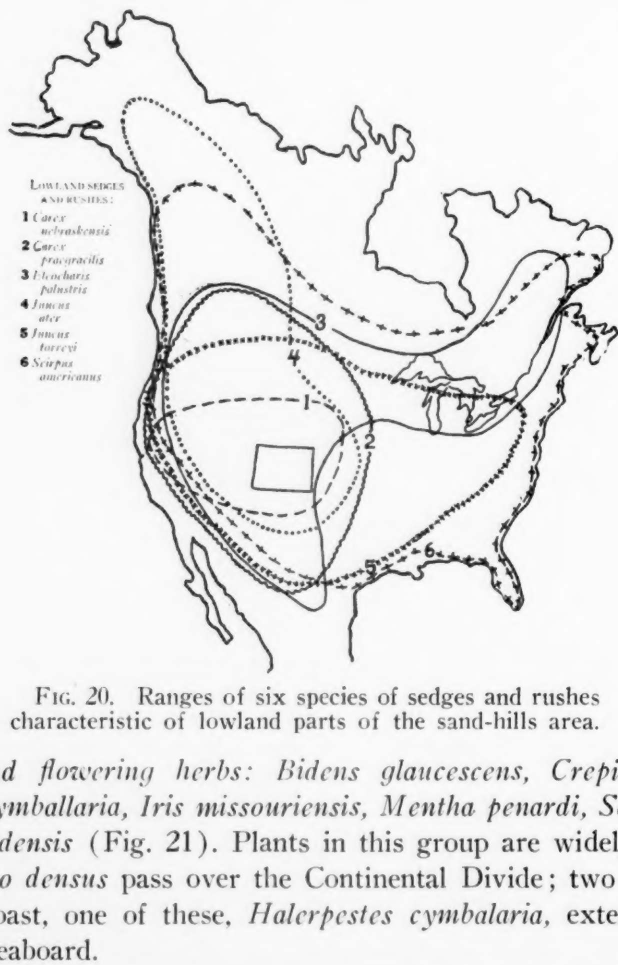

FIG. 20. Ranges of six species of sedges and rushes characteristic of lowland parts of the sand-hills area.

8. *Lowland flowering herbs: Bidens glaucescens, Crepis perplexans, Halerpestes cymballaria, Iris missouriensis, Mentha penardi, Senecio densus, Solidago canadensis* (Fig. 21). Plants in this group are widely distributed; all but *Senecio densus* pass over the Continental Divide; two species reach the Pacific Coast, one of these, *Halerpestes cymbalaria,* extending also to the Atlantic seaboard.

In general, a large portion of the characteristic species of the sand-hill district have a rather wide distribution extending to all points of the compass, and with few exceptions the Rocky Mountains do not limit their spread to the west. Upland plants have usually a more restricted range than plants of low areas, and flowering herbs as a rule do not have as wide a range as grasses. Many of the species range about the same distances in all directions, yet a few reach in the sand hills almost their northern limit and another

few their western limit—these latter not passing the mountains of the Front Range. Plants of loose sand and blow-outs are most circumscribed, while lowland sedges and rushes have the widest geographic range. This is to be expected, for it is well known that marshes are much alike while the very special xeric conditions of loose sand and blow-outs do not prevail over extensive areas. It is likewise to be expected that plants which are dominant or sub-dominant members in their community will range in all directions. Species near the outer edge of their geographic range are not often dominants —they are more likely to be rare or incidental constituents of the flora.

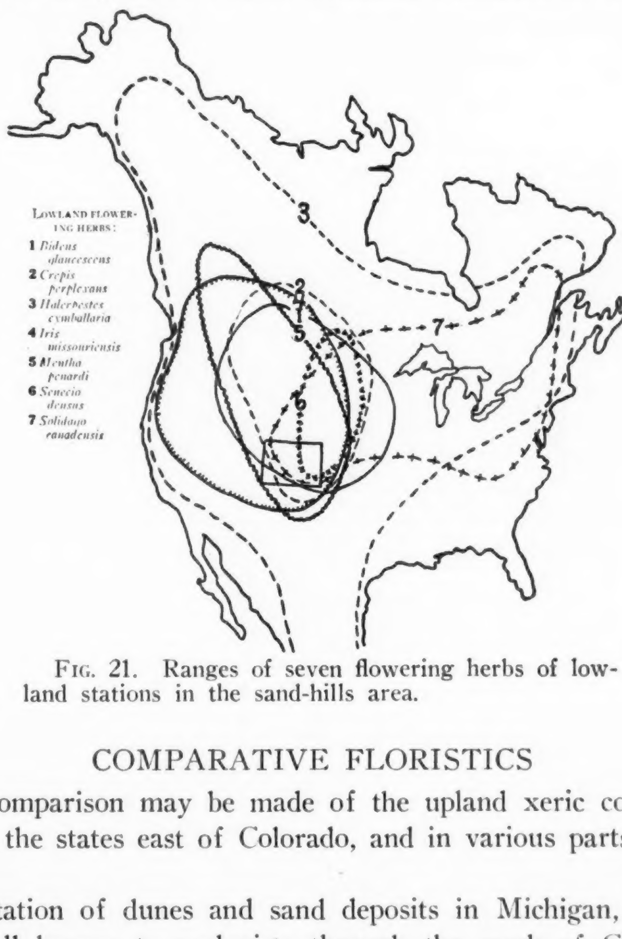

FIG. 21. Ranges of seven flowering herbs of lowland stations in the sand-hills area.

COMPARATIVE FLORISTICS

A brief comparison may be made of the upland xeric communities of sandy soil in the states east of Colorado, and in various parts of Colorado itself.

The vegetation of dunes and sand deposits in Michigan, Indiana, and Illinois is well known to ecologists through the work of Cowles, Fuller, Gleason, Peattie, and others, but these areas are so far removed geographically from Colorado that comparisons with them are not of great value.

Not so distant from Colorado are the dunes of Harrison County in western Iowa reported by Shimek (1917), where 88 species of vascular plants were collected; of this number, 16 species (18 per cent) occur also in the Colorado sand hills: *Equisetum kansanum, Typha latifolia, Elymus canadensis, Panicum virgatum, Cyperus schweinitzii, Scirpus americanus, Scirpus validus, Salix amygdaloides, Persicaria pennsylvanica, Cycloloma atriplicifo-*

lium, Chenopodium album, Trifolium repens, Melilotus alba, Solanum nigrum, Solidago canadensis, Lygodesmia rostrata. It is noticeable that these are all, save the last one, species not confined to xeric habitats. The highly xeric species of Colorado are not present in the more mesic climate of Iowa.

The prairie region of eastern Nebraska and adjacent states also may be considered for comparison with Colorado sand hills. Many of the grasses of the Colorado sand hills are of the same species, and nearly all are of the same genera as those of the prairie region enumerated by Weaver and Fitzpatrick (1934). Other plants, on the contrary, are very different; thus of the 75 species listed as the chief flowering herbs by these authors only one, *Allionia linearis,* is included in the Colorado sand-hill collections. Of the 51 genera, 22 have been collected by the present writer in the sand hills of Colorado.

In Clay County, Kansas, according to Schaffner (1926), sand hills occur as islands in the transition prairie. A list of 14 typical plants has 7 species which are in the present writer's collections from Colorado sand hills, viz.: *Calamovilfa longifolia, Sporobolus cryptandrus, Panicum* sp. (presumably *virgatum*), *Tradescantia occidentalis, Helianthus petiolaris, Cycloloma atriplicifolium, Plantago purshii.*

Small stands of an open plant community (Primitive Bunch-grass association, of Vestal) related to sand-hills prairie are described by Vestal (1914) as belonging to the mountain-front area in northern Colorado. They occur as scattered patches chiefly on deep sandy soil of railway rights-of-way and other undisturbed areas. The four species mentioned by Vestal are all present in the sand hills of northeastern Colorado, viz.: *Calamovilfa longifolia, Oryzopsis hymenoides, Panicum virgatum, Sporobolus cryptandrus;* but probably if flowering herbs also had been taken into account there would be some floristic differences.

Sand dune and sand-dwelling plants studied by the present author (Ramaley, 1919) near Georgetown, Colorado, at an altitude of 8,500 feet include many species which are present in the sand hills of northeastern Colorado, viz.: *Agropyron smithii, Distichlis stricta, Koeleria cristata, Oryzopsis hymenoides, Juncus ater, Capnoides aureum, Peritoma serrulatum, Chamaesyce serpyllifolia, Rhus trilobata, Plantago purshii,* and *Senecio spartioides.* Besides these there are species in the following genera which are ecologically closely related to species in the northeastern Colorado sand hills: Muhlenbergia, Stipa, Opuntia, Gilia, Artemisia, Chrysopsis, Machaeranthera, Solidago. Many of the species which are identical in the two localities attain at Georgetown almost their upper altitudinal limit, the sandy soil and protecting hills permitting lowland plants to reach this elevation of 4,000 feet above northeastern Colorado.

The Great Sand Dunes of the San Luis Valley in southern Colorado (Ramaley, 1929, also unpublished notes) furnish another area for comparison. These dunes are of enormous size, rising more than 700 feet above

the floor of the creek which flows at their base. Unlike those which form the subject of the present paper the higher parts of these dunes are almost altogether devoid of vegetation. Patches which are acres in extent may be bare sand. In protected depressions a very few species occur: *Oryzopsis hymenoides, Redfieldia flexuosa, Psoralea lanceolata, Helianthus petiolaris.* The lower parts of the dune area tend to have a shrubby vegetation: Grossularia, Ribes, and Chrysothamnus, with a moderate number of flowering herbs.

The contrasts which exist between grassland of the sand-hills area in northeastern Colorado and the prairie grassland of eastern Nebraska or that of mountain areas in northern Colorado result from environmental differences, both climatic and edaphic. The northeastern Colorado sand hills have less precipitation than the other areas, and a sandier soil than the mountain front, hence a more open community, fewer species, a generally greater xerophytism, and a larger proportion of more strictly sand-dwelling forms. The differences in species in comparing the sand vegetation of northeastern Colorado with that of the Great Sand Dunes in southern Colorado are accounted for by the proximity of this latter area to the arid Southwest—New Mexico and Arizona.

It is with the sand hills of central Nebraska that the greatest similarity to northeastern Colorado appears. All of the important species of the northeastern Colorado sand hills are present in Nebraska, but not all of the Nebraska species occur in Colorado. In Table 8 the floras are compared by listing the more important common species of each locality and indicating whether in the other locality the species is frequent, infrequent, or absent. Adding to the significance of the information, the comparison is extended to southern Colorado, that is, to the Great Sand Dunes and sand hills of the San Luis Valley. The table shows that the number of plants considered as important is greatest in Nebraska, fewer in northeastern Colorado, and least in southern Colorado, where the paucity of species is to be accounted for largely by the extremely arid climate and greater elevation—about 8,000 feet above sea level—with a consequent short growing season. Data on the Nebraska sand hills are from Pool (1914) with additional information furnished in a recent letter.

Vegetation of the wetter parts, quite as much as that of upland areas, is similar in the sand hills of Nebraska and of northeastern Colorado. Both have, among others: *Equisetum kansanum, Typha latifolia, Potamogeton* spp., *Alisma plantago, Sagittaria* sp., *Agropyron smithii, Agrostis hyemalis, Carex* spp., *Eleocharis acicularis, Eleocharis palustris, Scirpus americanus, Scirpus validus, Lemna trisulca, Juncus longistylus, Juncus torreyi, Polygonum amphibium, Batrachium trichophyllum, Halerpestes cymbalaria, Ranunculus sceleratus, Roripa* sp., *Berula erecta, Mimulus jamesii, Solidago canadensis.*

TABLE 8. COMPARISON OF SAND-HILLS AND DUNE FLORA IN CENTRAL NEBRASKA, NORTHEASTERN COLORADO, AND SOUTHERN COLORADO; DOMINANT AND PRINCIPAL SPECIES

Where species name is not given, the genus is represented by ecologically similar species. Pioneers of loose sand are distinguished by an asterisk (*); F equals frequent or common; I equals infrequent or rare; O equals absent.

	Northeastern Colorado	Central Nebraska	Southern Colorado
Agropyron smithii	F	F	F
Andropogon hallii	F	F	O
Andropogon scoparius	I	F	O
Aristida basirama	I	F	O
Aristida longiseta	I	F	I
Bouteloua hirsuta	I	F	O
Calamovilfa longifolia	F	*F	O
Eragrostis trichodes	O	*F	O
Koeleria cristata	F	F	F
Muhlenbergia pungens	F	*F	F
Oryzopsis hymenoides	*F	*F	*F
Panicum virgatum	F	F	O
Redfieldia flexuosa	*F	*F	*F
Sitanion hystrix	I	F	F
Sporobolus cryptandrus	F	F	F
Sporobolus cuspidatus	O	F	O
Stipa comata	F	F	F
Stipa spartea	O	I	O
Triplasis purpurea	O	I	O
Carex heliophila ("*pennsylvanica*")	I	F	O
Carex eleocharis ("*stenophylla*")	F	F	F
Tradescantia occidentalis	F	F	O
Juncus ater	F	I	F
Yucca glauca	F	F	F
Eriogonum annuum	F	F	O
Rumex venosus	F	F	I
Froelichia floridana	I	F	O
Cycloloma atriplicifolium	F	*F	F
Chenopodium oblongifolium	F	I	O
Abronia micrantha	I	I	F
Abronia sp.	I	F	O
Allionia linearis	F	F	F
Argemone intermedia	F	F	F
Lepidium alyssoides	O	O	F
Lesquerella sp.	F	I	F
Cristatella jamesii	*F	*F	O
Peritoma serrulatum	F	F	F
Ribes inebrians	O	O	F
Rosa sp.	I	F	I
Prunus besseyi	I	F	O
Amorpha canescens	O	F	O
Lathyrus sp.	I	F	I
Petalostemon villosus	F	F	O
Phaca longifolia	*F	*F	*F
Psoralea lanceolata	*F	*F	*F
Psorolea tenuifolia	I	F	O
Chamaesyce sp.	*F	*F	*F
Meriolix serrulata	I	F	O
Ipomoea leptophylla	F	F	O
Rhus rydbergii	F	I	O
Rhus trilobata	F	I	F
Ceanothus pubescens	I	F	O
Nuttallia stricta	F	F	I
Anogra cinerea	F	F	O
Collomia linearis	I	F	I
Gilia longiflora	F	I	F

TABLE 8 (Continued)

	Northeastern Colorado	Central Nebraska	Southern Colorado
Oreocarya suffruticosa	F	I	F
Pentstemon sp.	F	F	F
Lygodesmia sp.	F	F	F
Franseria acanthicarpa	F	F	F
Artemisia filifolia	F	F	O
Carduus plattensis	F	I	O
Chrysothamnus filifolius	O	O	F
Helianthus petiolaris	F	F	F
Helianthus subrhomboideus	O	F	O
Machaeranthera sp.	F	I	F
Othake sphacelata	F	I	O
Senecio spartioides	F	I	F

It must, however, be pointed out again that the Colorado sand hills are poor in number of genera and species. Many genera occurring in Nebraska are quite absent from the Colorado sand hills. Search through these hills has not brought forth examples of the following which occur in Nebraska sand hills: Dryopteris, Onoclea, Phalaris, Eriophorum, Lilium, Habenaria, Ibidium, Caltha, Impatiens, Menyanthes, Dodecatheon, Eupatorium. Further, genera which are often represented by only one or two species in Colorado may exhibit a half dozen species in Nebraska.

DISCUSSION OF COMMUNITIES

It is somewhat difficult to correlate exactly the plant communities recognized by the writer in northeastern Colorado with those of Nebraska—Pound and Clements (1900), Shantz (1911), Pool (1914). The difficulty is partly due to actual differences in the vegetation of the sand hills of the two states, and partly to differences in the minds of the various writers.

The sand prairie, as here understood, corresponds roughly to the Spear Grass (Stipa) Association of other writers, and it includes the Wire Grass Association and part of the Bunch Grass Association. It might be proper to consider this a consociation, a western modification of the prairie of the upper Mississippi Valley states; or, as the writer prefers, let it be called an association because of its wide extent and its distance from the true prairie.

The loose sand and blow-out community is essentially the Blow-out Association of the writers on Nebraska sand hills. In Colorado there are fewer species; if a considerable number of species enter the community it becomes "sand-hills-mixed."

The sand-hills-mixed community was originally given that name by Shantz; it resembles the Bluestem Type of Bunch Grass Formation and the Bunch Grass Association of the other writers, while it is practically identical with the *Muhlenbergia pungens* Association of Pool.

The sand sage community occurs in Nebraska as in Colorado; it is considered by Pool as a modification of the Bunch Grass Association. In Pound and Clements' Phytogeography of Nebraska it is named the *Artemisia filifolia* Formation.

The pondweed-arrowhead community is synonymous with Pool's Pondweed Association.

The cat-tail-bulrush community includes Pool's Bulrush-Reed grass Association and his Smartweed Association. This latter is not sufficiently developed in Colorado to deserve separate recognition.

The streambank community includes Pool's Streamside Marsh Association and his Water Hemlock Association and minor communities of Pound and Clements.

The sedge-rush marshland is the rush-sedge wet meadow of other writers.

The willow-poplar community, so feebly represented in Colorado sand hills, is the western extension of the various moist woodland communities of Nebraska. Its few poplars and willows are not sufficient in number to produce forests or groves; the following Nebraska trees are not present: Juglans, Ostrya, Xanthoxylum, Gymnocladus, Tilia—they do not extend west as far as Colorado.

The grass meadow of the Colorado sand hills, although poorer in species, is essentially the same as the hay meadow recognized by Pool, but does not exactly correspond to anything in Pound and Clements' Phytogeography of Nebraska.

Besides the absence of various woodland communities found farther east, the Colorado sand hills lack waterlilies to make a Waterlily Association and lack ferns to produce fern meadow.

The Short Grass and Grama-Buffalo Grass Associations of other writers and the Wire Grass Association of Shantz, the Wire Grass Transition Association of Pool, the Beard Grass Formation of Pound and Clements are not represented in the true sand hills of Colorado. They belong rather to hills or other rolling areas of compacted soil with considerable clay.

It may be well to state again, even at the risk of wearying the reader, that all of the communities of the Colorado sand hills are poor in species. They lack many of the species which extend west only as far as the Nebraska sand hills, and they have few or no western forms coming eastward from the Rocky Mountains.

SUMMARY

The sand-hill areas of northeastern Colorado in Weld, Morgan, Logan, Washington, Sedgwick, and Yuma counties support plant communities of restricted extent which appear over and over again in districts widely separated by many miles, and often with large intervening stretches of non-arenicolous flora. The dunes are of no great height, often 30 feet but seldom 50 or 60 feet tall.

Climate is typical of the high plains, with hot summers and cold winters; precipitation in most years is between 10 and 18 inches, but a large part falls in spring and summer, hence vegetation is not so xerophytic as might be expected in view of the low rainfall. The so-called "rain belt" of eastern Colorado has at times a rainfall of as much as 20 inches.

The total number of species of seed plants which may be considered as belonging to the sand-hills flora is about 140; the families represented by more than 6 species are Poaceae 32 species, Carduaceae 27, Fabaceae 19, Cyperaceae 11, Polygonaceae 9, Onagraceae 9, Chenopodiaceae 8, Polemoniaceae 7, Cichoriaceae 7. Many of the species, especially among the grasses, occur also in the shales and loess of ordinary plains, but some are generally or almost exclusively restricted to upland sandy soil, as examples: *Calamovilfa longifolia, Oryzopsis hymenoides, Redfieldia flexuosa, Eriogonum annuum, Rumex venosus, Cristatella jamesii, Lupinus pusillus, Petalostemon villosus, Phaca longifolia, Psoralea lanceolata, Ipomoea leptophylla, Gilia longiflora, Lygodesmia juncea.* Plants of wet sand are species of Carex, Cyperus, Eleocharis, Scirpus, Juncus, Sisyrinchium, Iris, Salix, Rumex, Persicaria, Sium, Verbena, Bidens. About one-third of all species in the sand-hills flora are true sand-dwellers, the other two-thirds belonging regularly to plains and prairies.

A sand prairie which may be called the Stipa-Andropogon-Calamovilfa Association forms the most advanced stage of sand-hill vegetation. This may be considered a western extension of the Prairie-Grass Association of Illinois, Iowa, eastern Nebraska, and Kansas. Typical "sand-hills vegetation" is, however, made up of persistent sub-climax communities belonging to the xerosere, chief among these being the sand-hills-mixed community dominated by *Muhlenbergia pungens* and the sand-sage community with *Artemisia filifolia* as the dominant plant. Pioneer species in blow-outs and fresh deposit-sand are *Oryzopsis hymenoides, Cristatella jamesii, Polanysia trachysperma, Phaca longifolia, Psoralea lanceolata, Chamaesyce* spp., and *Heliotropium convolvulaceum.* Valleys and sinks with typical moist-sand swamp and marsh plants become, with drying, grass meadows, these may pass slowly to the sand-prairie stage. The grass meadow is a long-lived community which has for its chief plants various species of Agropyron, Poa, and Carex, with *Hordeum jubatum, Panicum virgatum,* and *Spartina gracilis.*

Depressions, or sinks, within the sand-hill area have cat-tails and bulrushes in their moister parts surrounded with circum-areas of marsh and meadow. Older sinks have a dense growth of *Solidago canadensis.*

Sand hills which have become well stabilized take on a flora resembling that of the high plains, with the short grasses Bouteloua and Buchloe as dominants.

Besides recording the different plant communities, with their history, this paper includes quadrat and frequency studies, seasonal changes, climatic and

edaphic data, and general floristics; it is illustrated with photographs, charts, tables, and a topographic map of a typical sand-hill area near Roggen, Colorado.

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LIMNOLOGICAL STUDIES IN CONNECTICUT

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Presented in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy at Yale University.

CONTENTS

LIMNOLOGICAL STUDIES IN CONNECTICUT

INTRODUCTION

This is the first of a series of papers dealing with the limnology of the southern Connecticut region. It is a general survey, which was undertaken in order to determine the basic limnological features of a few representative Connecticut lakes.

The survey was begun in September, 1935, and was continued for slightly more than a year. Three lakes were studied—Linsley, Quonnapaug, and Quassapaug. Linsley was examined every two weeks and the other two once a month. Measurements were made of temperature, color, transparency, alkalinity, pH, oxygen, and the chlorophyll and organic matter in the plankton, and, in addition, a special study was made of the copper cycle in the three lakes. Detailed studies of the temperature, alkalinity, nutrient conditions, and plankton of Linsley will be presented in subsequent publications, the first three by Mr. G. Evelyn Hutchinson and the last by the present author.

I should like to thank Mr. Hutchinson for his invaluable suggestions and criticism throughout this work. I am also indebted to Dr. Oscar W. Richards for advice about statistical matters, to Mr. Hutchinson for permission to use his data on oxygen determinations, and to Mr. W. T. Edmondson and Dr. E. S. Deevey for aid in the collection of materials.

PART I. GENERAL LIMNOLOGICAL SURVEY

MORPHOMETRY

The lakes of southern Connecticut are all small and not very deep; the areas of the three studied varied from .1 to 1.2 square kilometers, and the maximum depths from 14.8 to 20 meters.

Maps of the lakes are shown in Figures 1 to 3. These were prepared from aerial photographs made by the Fairchild Aerial Survey Co. of New York City. The soundings were made by the usual limnological method of rowing across the lake in a straight line between two given points on the opposite shores, counting the oar strokes, and taking soundings at equal intervals. On the tracings from the photographs the lines of soundings were located, and contours were drawn. The area at the surface and at each contour was measured planimetrically, and the mean areas and volumes between successive contours were calculated.

TABLE 1. MORPHOMETRIC DATA.

	Linsley	Quonnapaug	Quassapaug
Location	North Branford	North Guilford	Middlebury
Area (sq. km.)	.094	.466	1.172
Volume (cu. m.)	$628.7.10^3$	2387.10^3	9758.10^3
Maximum depth (m.)	14.8	14.8	20.0
Mean depth (m.)	6.7	5.1	8.7
Area of drainage basin (sq. km.)	1.91	7.45	3.71
Lake area/basin area	.0494	.0625	.316
Elevation above sea level	25	53	212

TEMPERATURE

All three lakes are deep enough to be thermally stratified in summer, the maximum annual range in bottom temperatures lying approximately between 2.50 and 10.50°C. The thermocline in Linsley generally lies between three and six meters during the early summer months. In Quonnapaug and Quassapaug it is somewhat deeper, between five and eight meters.

The heat budgets and the values for stability and the work of the wind, shown in Table 2, are typical of small, shallow lakes.

TABLE 2. TEMPERATURE DATA.

	Linsley	Quonnapaug	Quassapaug
Annual heat budget (g.cal/cm^2)	10600	8500	15100
Work of the wind (g.cm/cm^2)	271	268	696
Stability (g.cm)	$21.6.10^6$	$18.9.10^7$	$33.6.10^7$

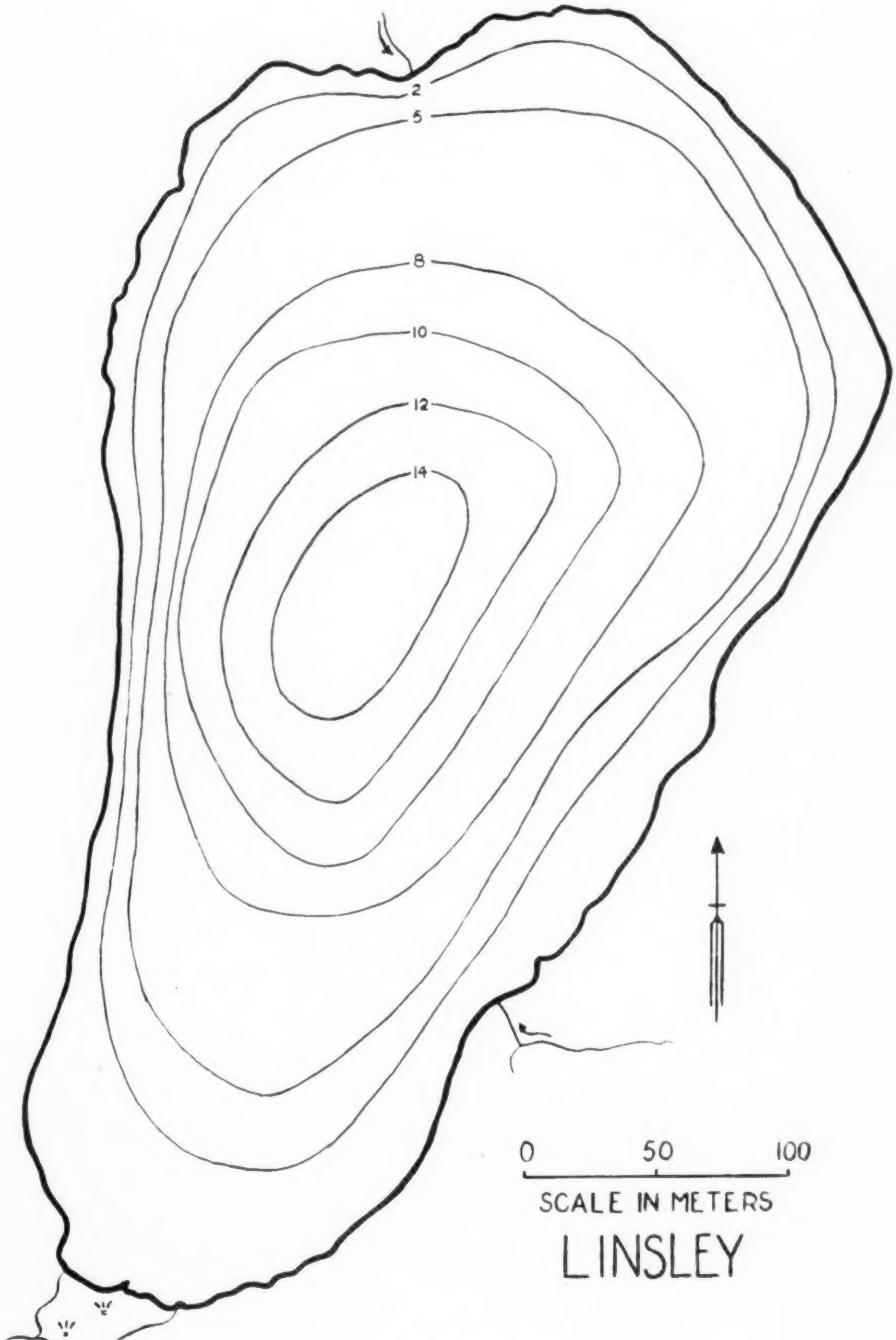

FIG. 1


0 100 200 300
SCALE IN METERS
QUASSAPAUG
2
8
12
16
18
16
14
14
12
10
8
5
2

FIG. 2

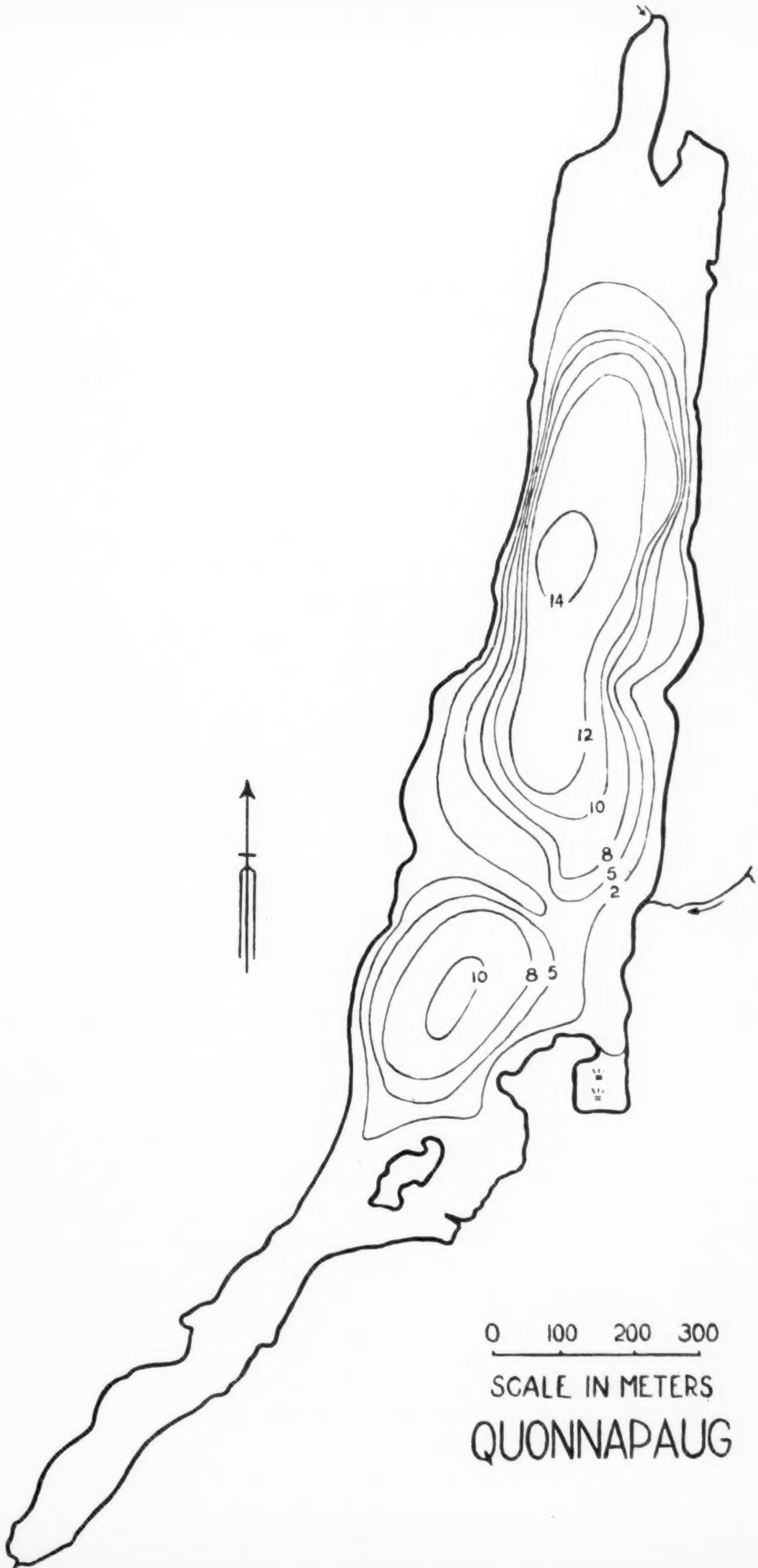

Fig. 3

TRANSPARENCY AND COLOR

The transparency, as measured by the Secchi disc, is a rough indicator of the amount of light available for photosynthetic processes. It is of course dependent on both the amount of light entering the lake and the transmission through the water.

The relations of transparency, color, and plankton, shown in Figure 4,

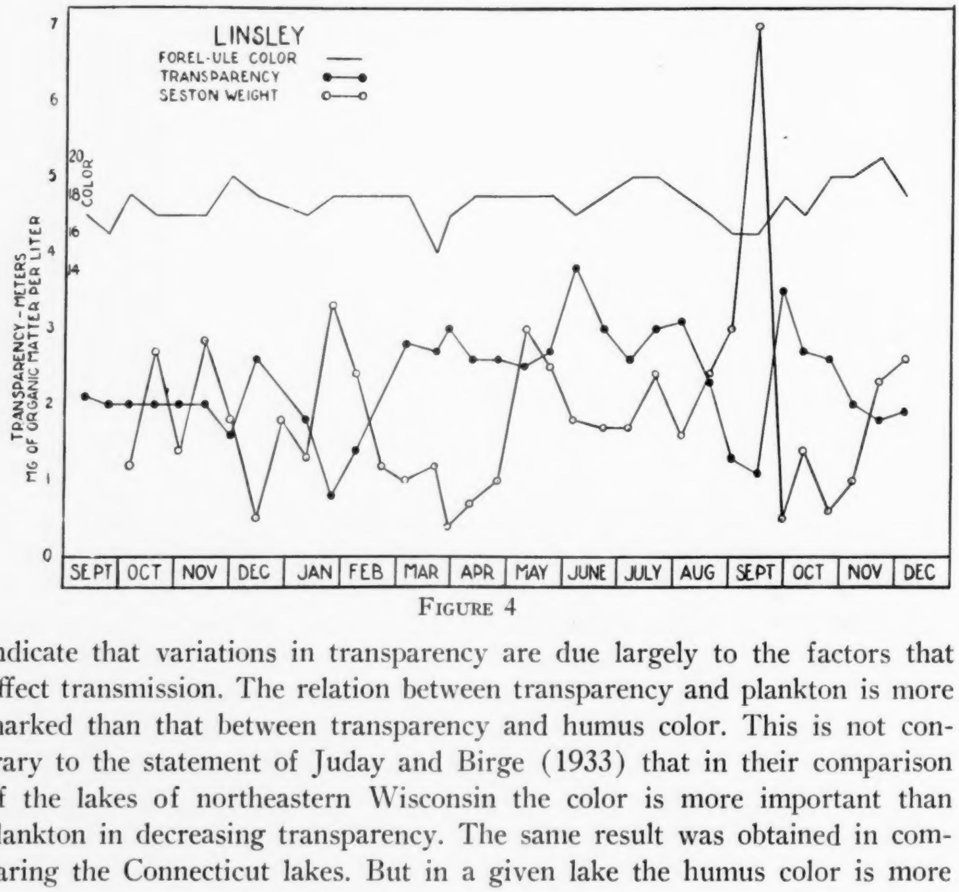

FIGURE 4

indicate that variations in transparency are due largely to the factors that affect transmission. The relation between transparency and plankton is more marked than that between transparency and humus color. This is not contrary to the statement of Juday and Birge (1933) that in their comparison of the lakes of northeastern Wisconsin the color is more important than plankton in decreasing transparency. The same result was obtained in comparing the Connecticut lakes. But in a given lake the humus color is more

TABLE 3. COLOR AND TRANSPARENCY.

	Linsley	Quonnapaug	Quassapaug
Color at the surface (U.S.G.S.)			
Maximum	35	30	5
Minimum	5	5	Trace
Mean	26	13	5
Forel-Ule color			
Maximum	20	19	10
Minimum	15	11	5
Mean	17.7	15.5	6.4
Transparency			
Maximum	3.8	4.6	10.5
Minimum	.8	1.7	3.4
Mean	2.3	3.7	6.0

nearly constant than the plankton, and consequently the latter is more important in causing minor fluctuations in transparency. Thus in Linsley the coefficient of correlation between plankton and disc reading was found to be —.585, while that between humus color and disc was only —.292.

The range of color and transparency in the three lakes is summarized in Table 3.

HYDROGEN-ION CONCENTRATION

The pH in Linsley is fairly constant, the maximum range being from 6.7 to 8.0 at the surface, and occasionally falling as low as 6.0 at the bottom. The pH stratification is in general direct, and the greatest difference between surface and bottom values occurs in the summer, with the arithmetical mean between the two about the same throughout the year. There are a few cases in Linsley of temporary dichotomy, such as those described by Yoshimura (1932). The average pH is slightly less in the other two lakes, the range being from 6.0 to 7.6.

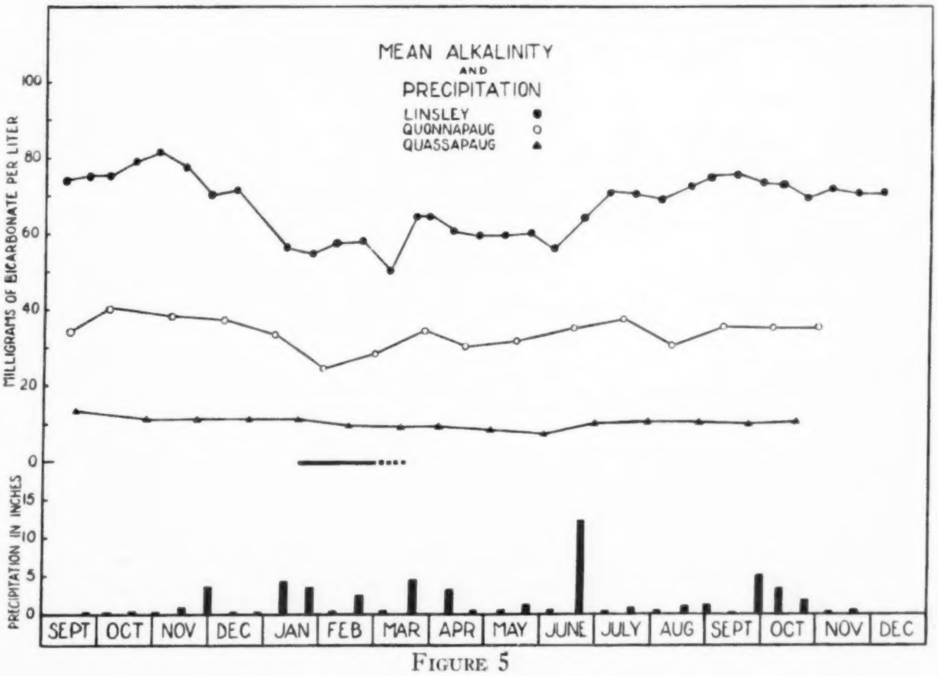

FIGURE 5

ALKALINITY

The variations in the mean alkalinity of the three lakes are shown in Figure 5. The precipitation is included on this graph, and the periods when there was snow on the ground and when it was melting rapidly in the early spring are represented by the horizontal line just beneath the Quassapaug curve. There is little relation between the amount of precipitation and the total alkalinity, but there were certain periods, particularly in March, when the ice and snow were melting rapidly, and in June, when the rains were unusually heavy, that decreases occurred in the surface water which can be ascribed to dilution effects.

OXYGEN

In Linsley and Quonnapaug the oxygen supply in the hypolimnion approaches depletion during the summer stagnation period, and therefore according to the classification of Thienemann (1928), they may be regarded as eutrophic lakes. In Quassapaug the hypolimnetic oxygen does not fall quite so low, and it is mesotrophic or on the borderline of eutrophy.

Strøm has suggested (1930, 1931, 1932, and 1932a) that in lakes in which the decrease of O_2 in the hypolimnion is largely due to the decomposition of dead plankton falling into it from above—i.e., in lakes which do not have a high relative amount of allochthonous organic matter—the increment in the deficit during a given period is roughly proportional to the plankton production during that time. The theoretical aspects of the problem have been treated in detail by Hutchinson (1938a). He showed that in four lakes—Green, Mendota, Furesö, and Black Oak—the ratios of absolute hypolimnetic deficits are 100:89:62:36, and the amount of organic matter in the mean standing crop of plankton per unit area is as 100:87:67:34. This close relation between deficit and plankton made it desirable to calculate the ratios for the Connecticut lakes, not only to test the hypothesis further, but also to provide a means of comparing the productivity of these lakes with that of lakes in other regions.

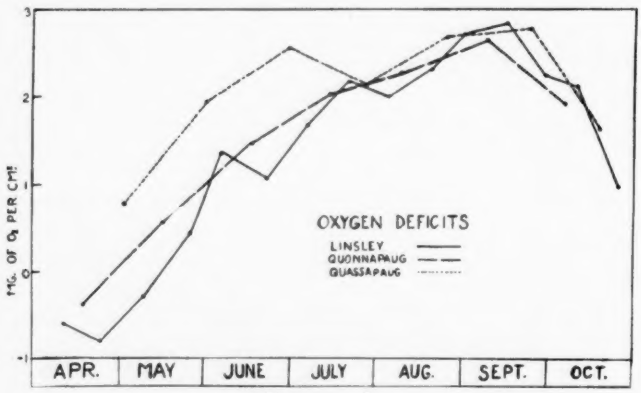

FIGURE 6

The calculations were done as follows: The oxygen curve at the time of full circulation was taken as the primary constant. This is considered preferable (Strøm, 1931; Hutchinson, 1938a) to Alsterberg's method of calculation. He defined the primary constant as the saturation value at the altitude of the lake at 4°C. The oxygen values for each successive date were then subtracted from the primary constant. The product of the deficits thus obtained and the volumes at the various depths were plotted, and the curve was integrated planimetrically to give the absolute deficit for each date. Only the hypolimnion was used for the calculations; the depths chosen for the upper limit of the hypolimnion were five meters in Linsley and Quonnapaug and 6.5 in Quassapaug. The absolute areal deficits (deficit per cm^2 of hypolimnetic surface) are shown graphically in Figure 6.

Continuing the ratios presented above, the deficit is as 20:16:11 in Linsley, Quonnapaug, and Quassapaug respectively, and the plankton is as 54:27:36. It is therefore obvious that the values for these lakes are not comparable with the other four, the amount of deficit accumulated per unit of plankton being much less. But while in Mendota, and probably in the other lakes, the deficit increases in an almost linear manner until the lakes begin to lose heat in August, in Linsley and Quassapaug the curves are broken by certain periods when the lake was gaining oxygen. In Quonnapaug, although there is not such striking evidence of gain in oxygen, the increase in the deficit is not linear. If the deficits are calculated for the spring and early summer, the part of the curves most nearly comparable to Mendota, the ratios are higher: 30:24:24. Quonnapaug now fits with the other data, but the other two are still too low. In Linsley it is only during the period from May 23 to June 6 that the values for deficit and plankton are comparable (52 and 54), and the deficit in Quassapaug from May 2 to June 1 is almost as high as the plankton (30 and 36).

It must therefore be concluded that in these shallow lakes the deficit is not an accurate measure of productivity, and that only on rare occasions does the increment in the deficit approach the higher values found in deeper lakes. The most likely explanation of this increase in hypolimnetic oxygen is pseudo-oligotrophy (photosynthesis in the hypolimnion). Hutchinson (1938) has shown that vertical mixing in the hypolimnion of Linsley is negligible during the summer stagnation period. The periods of decrease in the deficits of the three lakes correspond to chlorophyll maxima. And finally, recent measurements of oxygen production and consumption in submerged bottles of lake water show that during the autumn and early winter photosynthesis occurs in Linsley at a depth of thirteen meters. But whether production in the hypolimnion ever exceeds consumption during the summer has not yet been determined.

It is probable that these lakes, although eutrophic from the standpoint of the oxygen curve, are not highly productive. Values for the deficit obtained over short periods of time, which seem from comparison with the plankton to represent the potential deficit for each lake, indicate that Linsley occupies a position about midway between the highly eutrophic Wisconsin lakes and the less productive ones of northeastern Wisconsin, and is probably within the range of the Baltic lakes. Quonnapaug and Quassapaug both fit into the group of Wisconsin soft water lakes. They are therefore mesotrophic according to the classification of Hutchinson (1938), and Linsley lies in the lower range of eutrophy.

This conclusion is supported by the plankton investigations. It is generally true that in eutrophic lakes there are plankton blooms at some time during the year, but they do not occur in mesotrophic or oligotrophic lakes. In Linsley there were extensive blooms in August and September, com-

posed chiefly of the blue-greens *Anabaena, Coelosphaerium,* and *Microcystis.* In the other two lakes water blooms were not found.

PLANKTON

Plankton studies included chlorophyll analyses and the determination of the dry weight of organic matter in the seston. The latter was removed from the water by means of a thirty-five second membrane filter.

The chlorophyll analysis as a routine measurement of phytoplankton was introduced by Harvey in 1934. The method used here (Riley, 1938) differs from his only in that the chlorophyll is separated from the carotinoids, which are frequently present in fresh water in sufficient quantity to obscure the chlorophyll color and make colorimetric determinations difficult and inaccurate. The chlorophyll determination is the simplest method available for determining relative quantities of phytoplankton and is therefore extremely useful in routine surveys. Work now in progress in this laboratory indicates, however, that the ratio of chlorophyll to cell volumes varies according to the physiological activity of the cells and the type of organisms that compose the plankton. It is not yet possible to state which one of the several available methods is best, but it is evident that in a detailed plankton survey, as in other growth studies (Richards, 1933), it is necessary to use more than one criterion.

The weight of organic matter is a better index than chlorophyll of the total productivity of a lake because the latter must include an estimate of animal production. For example, in Quonnapaug the mean amount of chlorophyll at the surface is 10.5 Harvey units per liter, and in Quassapaug it is 7.5. But the total weight of organic matter is greater in Quassapaug. The Quassapaug plankton contains a greater quantity of animals, and their feeding is at least partly responsible for the small standing crop of phytoplankton, so that the relative quantities of chlorophyll in the two lakes cannot be regarded as proportional to the actual productivity. The oxygen deficits indicate that Quassapaug is actually more productive than Quonnapaug, and the ratio of the deficits is approximately the same as the organic matter ratio. In Linsley the relative quantities of chlorophyll and organic matter are about the same as in Quonnapaug, but the actual quantity of phytoplankton is about 70% higher, which is sufficient to make it more productive than either of the other lakes.

The ratio between chlorophyll and organic matter is of some interest. The mean ratio for the entire year varies in the three lakes from 5.7 to 9.4 (Harvey units per liter: mg. of organic matter). It becomes higher during periods of pronounced phytoplankton growth (11—28). The ratio decreases during stagnation periods, and becomes very high during overturns (11—34).

If one were to assume that at the time when the ratio is very high the phytoplankton is the only constituent present, the total weight of organic matter would be the weight of organic matter in the chlorophyll-bearing

phytoplankton, and it would then be possible to estimate the weight of phytoplankton for the entire year by applying this ratio to all the chlorophyll determinations. The estimate is included in Table 4 with the summary of the chlorophyll and organic matter determinations. The estimate is probably too high because of the systematic error of the primary assumption, but even so, the quantity of living phytoplankton appears to be rather small (17-28% of the total).

TABLE 4. PLANKTON.

	Linsley	Quonnapaug	Quassapaug
Chlorophyll (Harvey units per liter)			
Maximum	70.5	27.6	15.1
Minimum	5.0	4.2	1.7
Mean	17.47	10.49	7.45
Seston weight (Mg. per liter)			
Maximum	7.0	1.9	3.0
Minimum	.4	.4	.2
Mean	1.94	1.12	1.31
Estimated weight of phytoplankton (Mg. per liter)			
Maximum	2.14	.81	.44
Minimum	.15	.12	.05
Mean	.53	.31	.22

Another method of estimating the weight of phytoplankton is to calculate the relationship between variations of organic matter and chlorophyll. The regression equation for Linsley, obtained by the products moments method, is

$$X = .026Y + 1.49$$

where X is the weight of organic matter in milligrams per liter, and Y is Harvey units of chlorophyll per liter. According to this equation, the weight of phytoplankton in Linsley varies from .13 to 1.83 mg. per liter, and the mean is .45, or 23% of the total. This method is accurate if the other constituents of the seston vary independently of the phytoplankton. If, on the other hand, a direct relationship exists, that part of the non-chlorophyll-bearing seston that varies with it will be included in the estimate. Since the latter is undoubtedly partly true, this estimate is also slightly too high.

These results must therefore be regarded as theoretical maximum values for phytoplankton. With more accurate methods the estimate would be lower. Ruttner (1937) found that in ten east Alpine lakes the volume of phytoplankton ranged from .07 to 2.62 mm^3 per liter in the surface waters, with an average of .56 mm^3. Assuming that the dry organic matter of the plankton was about ten per cent of the wet weight, he estimated that the phytoplankton averaged about .056 mg. per liter, a figure in striking contrast to the usual range of seston weights. The various methods of evaluating the crop of living plankton are now undergoing further investigation and will be discussed in detail in a subsequent publication.

In these lakes there is little evidence of a seasonal variation in plankton, which is dependent on nutrients regenerated during periods of overturn. It is evident from examination of Figure 7 that there is a tendency

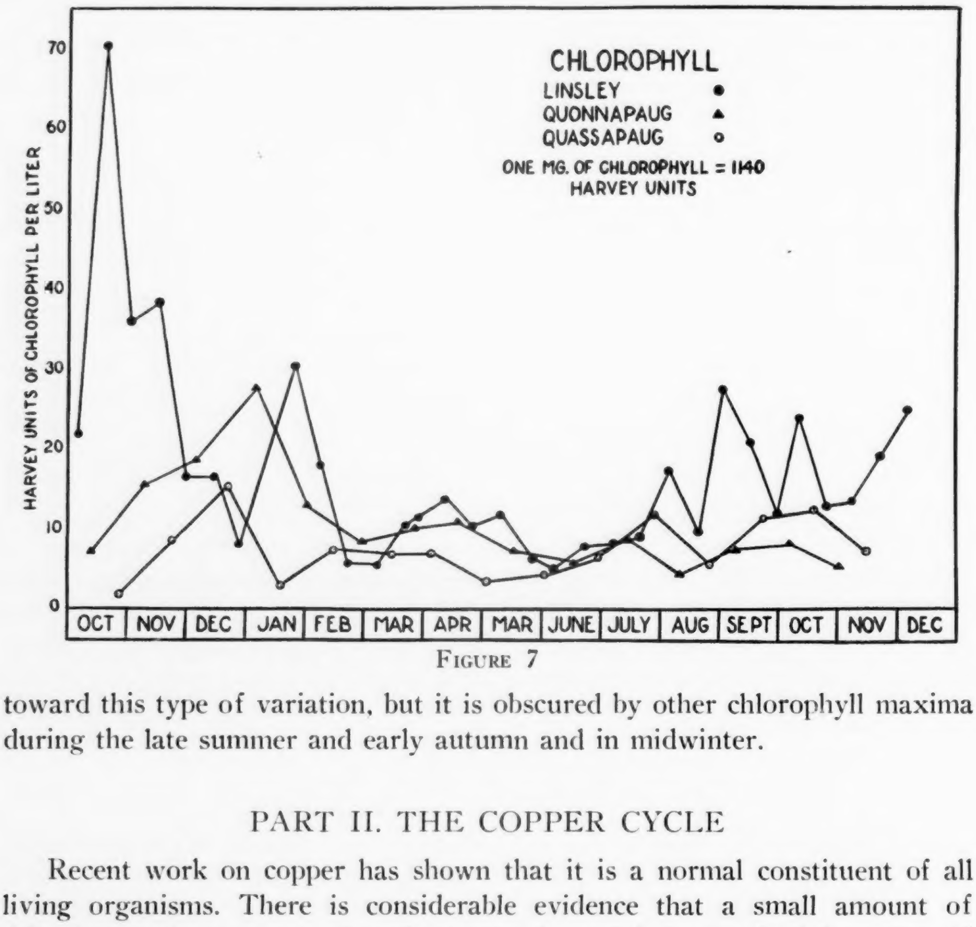

FIGURE 7

toward this type of variation, but it is obscured by other chlorophyll maxima during the late summer and early autumn and in midwinter.

PART II. THE COPPER CYCLE

Recent work on copper has shown that it is a normal constituent of all living organisms. There is considerable evidence that a small amount of this element is necessary for plant growth, and it is required by some, if not all, animals.

On the other hand, a slight increase of copper in the diet or the fluid medium has a strongly toxic effect, and it has been used extensively in agriculture and in municipal water supplies to eradicate undesirable organisms of various sorts.

Thus the amount of copper in the environment might conceivably be important biologically because of either deficiency or excess. The present work was undertaken in an attempt to discover whether or not, in a normal aquatic environment, it appeared to be a significant limiting factor from either of these standpoints. The study consisted of determinations of the copper distribution at regular intervals for slightly more than a year, and this was followed by laboratory experiments with aquatic animals to determine their tolerance to varying amounts of copper in the medium.

THE MEASUREMENT OF COPPER CONTENT

The method chosen for this work was introduced by Callan and Henderson in 1929. The reagent is sodium or potassium diethyldithiocarbamate, $(C_2H_5)_2N.CSSNa$, the copper salt of which has a golden brown color in aqueous solution. The range of sensitivity of the method as originally described lay between .02 and 1 ppm., but subsequent modifications have increased the sensitivity considerably. This was accomplished by Haddock and Evers (1932), who suggested extraction of the copper salt with carbon tetrachloride, concentrating it about tenfold. Two other solvents were later introduced: chloroform (Atkins, 1933) and amyl alcohol (McFarlane, 1933). The latter was used in this investigation.

The method as applied to limnological work is as follows: For the determination of copper ion, to 50 ml. of lake water one-half ml. of a saturated solution of Na diethyldithiocarbamate and about 5 ml. of amyl alcohol (see below) are added. The mixture is shaken thoroughly, and the amyl alcohol is allowed to separate from the water. It may then be drawn off and compared colorimetrically with a standard copper solution prepared in the same manner. For the determination of total copper, 20-50 ml. of water are evaporated in a quartz dish, and the residue is heated in an electric kiln until all organic matter is destroyed. The ash is then dissolved with .5 ml. of hot 12 N HCl, the solution is made up to 50 ml. with water, and the copper is determined in the same manner as described above.

In practice it has been found convenient to use a .001 N solution of potassium dichromate as an arbitrary standard. It has the same tint as the copper solution throughout its entire range, and the color varies proportionally. It thus saves one from making up a standard copper solution for each set of analyses and from the error of the preparation.

The quantity of amyl alcohol used is 4.97 ml. This amount was chosen arbitrarily because it produces a depth of color equivalent to that of a thousandth Normal dichromate solution when used to extract a copper solution of .03 mg. per liter. This is a good working value since it lies approximately in the middle of the usual range of determinations. Thus, by setting the solution to be tested at 30 on the colorimeter and adjusting the dichromate to the same depth of color, its scale reads directly as thousandths of a milligram of copper per liter of water in the unknown.

The range of sensitivity for determination of the copper in a 50 ml. sample of lake water lies between .002 and .1 mg. per liter. For total copper the range may be extended almost indefinitely in either direction by varying the size of the sample used. The error of the method is about three per cent.

It is of course necessary to run blanks on the reagents and make corrections when they show contamination. With the use of pyrex distilled water and the ordinary reagent grade of HCl these corrections are generally negligible.

Atkins (1933) was unable to use amyl alcohol as an extractive agent because it dissolved humic matter from the water, which of course gave an erroneous figure for copper. I have not had this trouble, probably because the waters dealt with here are clearer.

The color is developed equally well throughout almost the entire pH scale. This facilitates the estimation of total copper, for the acid solution does not need to be neutralized.

Lead, zinc, and iron interfere with the copper determination. Of these, only iron is ever present in sufficient quantity to be troublesome, and then only in the bottom waters. It may always be detected by a reddish tint in the solution. During the course of several hours it fades, and the copper solution, which is stable for at least three days, may then be tested, making a small correction for residual iron equivalent to .003 mg. per liter of Cu. This approximation is better than the usual procedure of removing the iron with citrate and ammonia (Haddock and Evers, 1932), because the ammonia disturbs the copper equilibrium in lake water and brings more of it into ionic form.

Interference occurs only in the estimation of copper ion and never causes difficulties after evaporation and ignition of the water sample, perhaps because ferric chloride boils off or possibly by the formation of highly insoluble iron silicates.

In addition to the determinations of soluble and total copper, a test is made of the total copper in a filtrate which has passed through a thirty-five second membrane filter. Thus it is possible to fractionate the determinations into four sets: soluble, seston, organic and colloidal, and total copper. The term seston copper refers to the fraction contained in particulate matter which is greater than $.6\mu$ in diameter. It thus includes the copper in plankton, organic detritus, and inorganic particles.

The organic copper represents not only that in organic combination but also the copper attached to particles smaller than $.6\mu$. It is possible to fractionate the copper distribution still further by the use of filters of various sized pores, but this requires too much time to be practicable as a routine procedure. On two occasions the greater part of the colloids were removed by the use of a fine ultra-filter (McDonald's Pond, Sept. 28, 1935, and Linsley, Nov. 30, 1935). The colloidal copper was greatly in excess of the organic fraction: in the former .039 and .009 mg./1., and in the latter .070 and .018, the colloidal copper constituting 81.3% and 79.5%, respectively, of the total.

THE OCCURRENCE AND DISTRIBUTION OF COPPER IN CONNECTICUT LAKES

General Data

The best records of the occurrence of copper in fresh water have been obtained recently by Atkins (1933), Prytherch (1934), and Braidech and

Emery (1935). The last two authors listed about twenty-five municipal water supplies in the United States of which they made copper determinations by the semi-quantitative spectrographic method. Their values ranged from .005 to .6 mg. per liter.

None of the Connecticut lakes examined during the present survey gave a negative test for total copper. The content varies tremendously with the season and from one year to the next, the total range in all the analyses being from .009 to .383 mg. per liter. It is quite possible that with longer study the range might be even greater.

A summary is presented in Table 5 of analyses made at regular intervals from September, 1935, to January, 1937:

TABLE 5. GENERAL DATA ON COPPER.

	Linsley	Quonnapaug	Quassapaug
Cu ion—epilimnion	.005–.035	.004–.033	.004–.024
Cu ion—entire lake	.005–.066	.004–.099	.004–.028
Total—epilimnion	.011–.215	.009–.083	.010–.203
Total—entire lake	.011–.383	.009–.370	.010–.203
Seston Cu	.000–.163	.000–.196	.000–.076
Organic Cu	.000–.187	.000–.109	.000–.117

Vertical Distribution of Copper

Figure 8 shows distribution curves in Linsley selected from data taken between Mar. 7 and Sept. 15, 1936. It may be seen that in the early spring (Figure 8, A to C) the concentration of soluble copper is very nearly uniform from surface to bottom, but from April 25 (D) until the end of the summer stagnation period there was a slight accumulation of soluble copper in the hypolimnion. The same thing occurred in the winter under the ice (H, Mar. 7, 1936).

The distribution of total copper was highly irregular, and this was especially marked during overturns. After the spring overturn of 1936 there was a rapid decrease of total copper in the bottom waters resulting in an inverse stratification on Mar. 28 (B). Throughout April the amount at the surface decreased steadily, with the maximum appearing at successively lower levels. Persistence of this type of phenomenon would lead to pronounced accumulation of copper in the hypolimnion. But it is evident from the examination of the subsequent curves that not only is the accumulation in the bottom waters not as great as in the case of some other elements, such as phosphate and iron, but that occasional increases of copper at the surface cause partial or complete inversion of the curve. On May 23, Aug. 4, and Aug. 19 complete inverse stratifications occurred, and partial inversions resulting in dichotomous curves were found on May 9, June 22, Sept. 1, Sept. 15, Sept. 29, and October 10. The curves for June 22, Sept. 1, and Sept. 15 are shown in Figure 8, E, F, and G.

Between these periods of increase at the surface there was a tendency toward resumption of the direct type of stratification, in which the concentration of copper became greatest at the bottom or at some intermediate point. For example, comparison of F and G shows, in the latter, a decrease in copper at the surface and a corresponding increase at the bottom.

During the winter the distribution tends to become uniform except just above the bottom, where there is a slight accumulation. This condition is shown in H, Mar. 7, 1936, about a week before the end of the winter stagnation period.

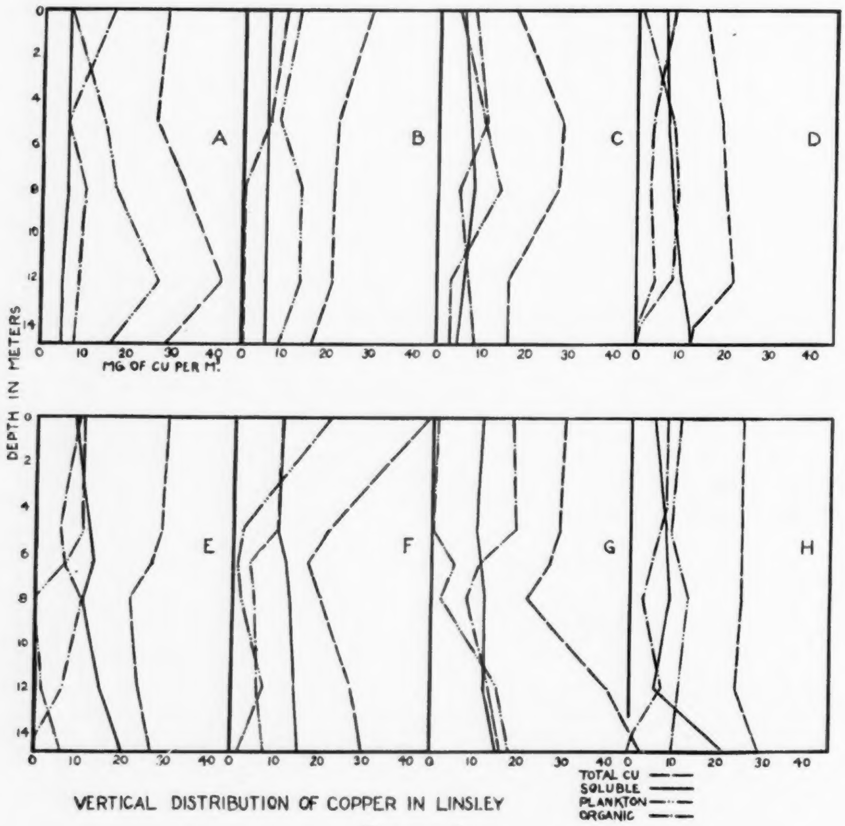

FIGURE 8

The seston and organic copper appear to be highly labile; their variations tend toward an inverse relationship.

The same types of vertical distribution were found in Quonnapaug and Quassapaug. On the whole, the variations were less in these lakes, and this was especially true of Quassapaug.

Seasonal Distribution of Copper

In order to evaluate the seasonal cycle of copper it was necessary to calculate the total amount of copper in the lake on each date, following the methods of enumeration used by Thienemann (1928) for oxygen and by Yoshimura (1930, 1931) for silica, iron, and other substances. Where the

variations between successive strata were very irregular this was done by drawing the curve of vertical distribution and integrating planimetrically, but in most cases it was sufficient to interpolate between successive levels.

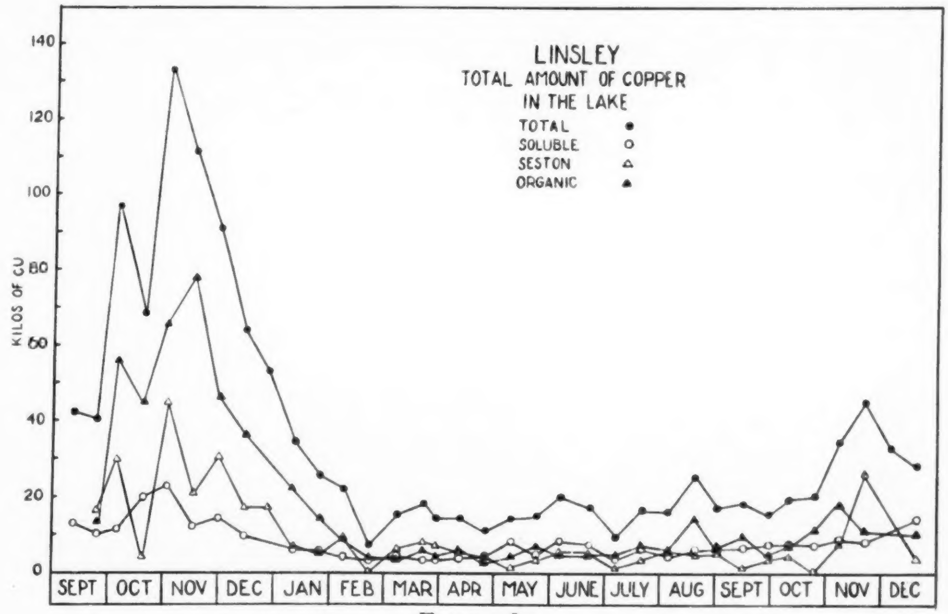

FIGURE 9

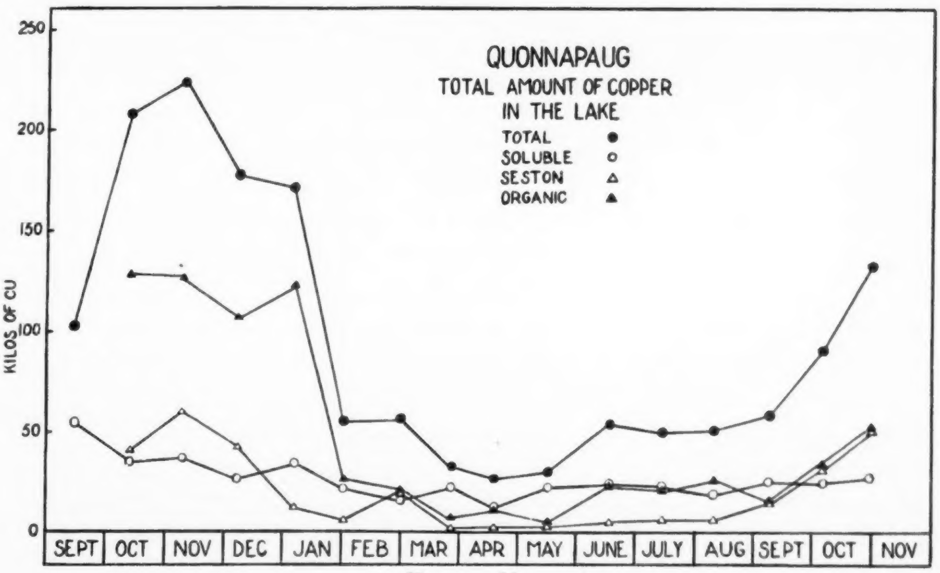

FIGURE 10

The results are shown in Figures 9 to 11. It may be seen that the annual variation is extreme, the copper being greatest in the autumn and least in the late winter and spring. The cycles are roughly similar in all three lakes, but there are numerous variations that are undoubtedly caused by local conditions. The agreement between the Linsley and Quassapaug curves is especially marked, the chief difference being minor variations over short

periods of time in Linsley which are not recorded in Quassapaug, partly because the analyses were made at longer intervals, and also because Quassapaug, being less productive and in general more stable from the chemical standpoint, could hardly be expected to change so rapidly.

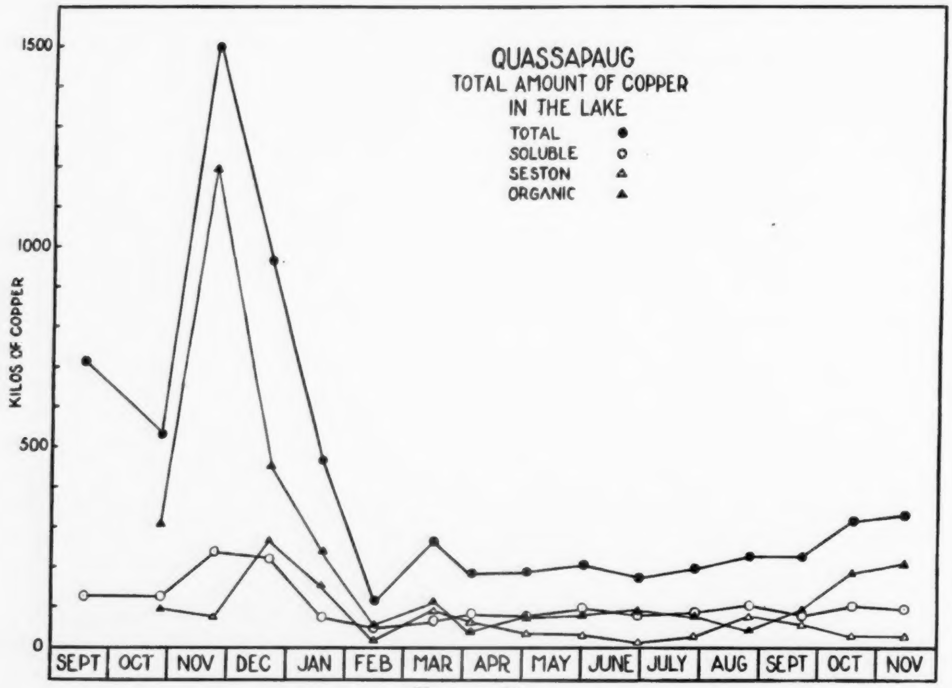

Figure 11

Factors Influencing the Distribution of Copper in Lakes

The copper in natural waters is derived ultimately from the soil of the drainage basin. All soils contain copper, ranging from a trace to several per cent, and ground water dissolves traces of copper from the relatively insoluble salts in the soil and eventually brings it into streams and lakes. The amount coming into a body of water is dependent on several factors: the quantity in the soil, its availability, and the amount of precipitation.

In a given lake basin the first two factors are nearly constant and may be ignored, while on the other hand they are of primary importance in the comparison of lakes in different regions. If the data of Braidech and Emery (1935) of analyses of water from various parts of the United States can be regarded as an accurate index of the availability of copper in those regions, it is apparent that mountainous regions are lowest except where there are ore deposits, in which case the availability is very high. Regions of sedimentary deposits tend to be lower than igneous, and lowland soils with high organic content have little available copper. These factors suggest that the availability in Connecticut soils is above average.

The effects of precipitation can be shown by comparing the figures for rainfall with the copper content of water entering the lake. The data for

the winter period are not used because of the obvious inaccuracy of estimating the lag period for melting, and the autumn data are also omitted because, as will be shown later, decaying plants at that time liberate copper, thus introducing a complicating factor not related to the soil-precipitation problem.

There are eleven sets of analyses of the inlets between April 11 and September 15, 1936, spaced at two-week intervals except for one gap in the July data. In six of the analyses the copper is lower in the inlets than in the lake, in four it is about the same, and in one it is higher. In the first set the mean rainfall in the two-week period preceding the analysis was 3.19 inches. In the four cases where the copper content of lake and inlets was about the same, the mean precipitation was .70; in the one case where it was higher, the rainfall measured .53. It therefore appears likely that there is an inverse relation between the amount of precipitation and the copper in the inlets. If that is so, heavy rains would tend to dilute the lake water and lower its copper content.

In a recent unpublished investigation of the relations of precipitation to the lake level and the volumes of the inlets and outlet, Hutchinson has shown that the effect of a rain is evident on the following day, and the effect is largely dissipated by the fourth day. According to this, the effect of precipitation on copper content would occur during the following week. If, however, rains were frequent over a period of several weeks, the diluting effect might be cumulative. Since the precipitation during the period in question showed a cyclical tendency, it was desirable to test the hypothesis.

During the period from September 24, 1935, to November 21, 1936, the coefficient of correlation between the decrease in copper in the lake since the preceding analysis and the precipitation during the previous week was .124. For the second week previous to the analysis it was .155, for the third .189, and for the fourth .004. Using the total rainfall during the three weeks previous to the analysis, the correlation was increased to .276. Since the probable error for these correlations is .119, none of the results are statistically significant. The highest one falls into the 12% level of probability. When only the data for the spring and summer period are used, the correlation is increased to a significant level ($r = .500$). It is therefore evident that precipitation tends to lower the copper content of the lake during the summer stagnation period, and the effect appears to be cumulative, but during the rest of the year it is of little or no importance.

Reactions of Copper in the Lake

If copper were inert biologically and chemically, one would expect that the amount in a given lake would remain fairly constant, and that any variations which occurred would be dependent on the concentration of copper in the inlets and ground water, which in turn would be related to the quantity of precipitation. But this is not the case.

In the first place, the correlations mentioned above are not high enough to warrant the assumption that precipitation is solely responsible for variations in copper.

Second, large variations take place too rapidly to be thus accounted for. For example, the peak of the autumn maximum of 1936 occurred on November 21, when the copper in the lake measured 45.6 kilos, an increase of 125% in four weeks. At that time the volume of water passing through the lake, determined by measurement of water flowing through the outlet, was about 8000 m^3 per day. In order to produce an increase of that magnitude it would have been necessary for the copper content of the water entering the lake to average .165 mg. per liter. The amount actually in the inlets during this period ranged from .024 to .069.

Measurements of ground water were made by thrusting glass tubes into the bank about twenty or thirty centimeters below the lake surface. They were partly plugged at the ends to prevent wave action from creating currents in the tubes and were tilted up so that the colder ground water would remain in the tubes and gradually replace the lake water. One tube was used to collect a water sample, another to test the rate of flow by means of a little eosin placed in the proximal end of the tube. While this method could never be completely accurate, some of the results appeared to be reasonably satisfactory. During the period in question, the highest value obtained for copper in the ground water was .078 mg. per liter. It therefore appears that the major variations of copper cannot be accounted for on the basis of precipitation effects, but are at least partly due to reactions in the lake basin. It will be shown that these reactions may take the form of either removal or regeneration.

Removal of Copper from Lake Water

It was believed by the older workers that when copper was put into lakes it was precipitated rapidly. They postulated the formation of insoluble salts such as the hydroxide, carbonate, phosphate, and sulfide; this apparently was not proven by experiment but was advanced merely as a possible explanation for the fact that copper when added to lake waters disappeared rapidly from solution.

My own work does not confirm this viewpoint, but indicates rather that the chief means of removal of copper from solution is adsorption on organic particles. For the adsorption experiments natural waters with high humus content were used. Five hundred milliliters were taken from the larger inlet at Linsley on Oct. 24, 1936. This water had a color of 150 and a pH of 6.9. The organic matter was 122 mg. per liter, the soluble copper .011, and the total Cu .032. .2 mg. of copper was added to the 500 ml., making the total content .432 and the ion .411 mg./l. The temperature was 21.9 at the beginning of the experiment, but it was not controlled and probably varied considerably. The amount of ion was then tested at intervals for

two days to find the amount of removal. A large part of the copper remained in solution, and it appeared desirable to do another experiment of the same type, adding less copper to see if more complete removal was obtained. This experiment was performed on Jan. 16, 1937, under the same conditions except that the temperature was controlled accurately. The results of the two experiments are shown in Table 6.

TABLE 6. COPPER ADSORPTION EXPERIMENTS.

October 24, 1936		January 16, 1937	
		Organic matter 60 mg./l.	
		Sol. Cu. .010, total .032	
8:40 A.M.	.411	8:45 A.M. ... ion increased to	.110
8:45	.404	8:50	.100
9:20	.380	9:08	.091
10:00	.353	9:35	.085
11:00	.337	10:10	(?).110
12:00 M.	.319	10:25	.078
1:30 P.M.	.315	11:20	.076
3:30	.308	12:45 P.M.	.075
7:40	.298	4:10	.073
8:40 A.M. 10/27	.288		
10:00 A.M. 10/28	.276		
3:00 P.M. 11/7	.360		
		Temperature 25 ± .1°C.	

It was pointed out by Freundlich (1922) that one of the most characteristic features of the adsorption process is that the amount taken up does not bear a linear relationship to the concentration. This is the case here. The concentration in the first experiment was 3.72 times as great as in the second, and the amount of removal was only 2.03, if allowance is made for the difference in the quantity of organic matter in the two solutions. It was therefore advisable to test the data further to see if the removal was a simple adsorption phenomenon. Freundlich's equation for adsorption is

$$\frac{x}{m} = \alpha . C^{\frac{1}{n}},$$

where x is the amount adsorbed, m is the adsorbing surface, and C is the final concentration of the solution. α and $\frac{1}{n}$ are constants for a particular surface and solution. m is also regarded as a constant here; it is impossible to state its absolute value because it consists of particles of all sizes. Failure to use it prevents calculation of the other two constants, but it is considered permissible to treat the data in this way in order to find the type of curve produced, because there is no reason to believe that m changes during the course of an experiment.

Log x/m plotted against log C typically gives a straight line for the adsorption phenomenon. In these experiments straight lines are obtained, but there is a sharp break in each curve (Figure 12). This is characteristic of adsorption from solutions of high concentration. Here a break would be

expected, because in natural waters there is already an equilibrium established between ion and adsorbed copper, and the adsorption experiment is merely a process of raising the equilibrium to a higher level. It is therefore inevitable that the surface becomes "saturated" toward the end of the experiment.

It will be evident later in the discussion that certain variations of copper in the lake basin are most readily explained by the assumption that organic matter easily removes copper ion from solution. The experiments lend plausibility to the assumption. There is one other type of phenomenon that obeys the adsorption formula: namely, the partition of a substance between two immiscible solvents, where the solubility is unequal and conforms to a definite

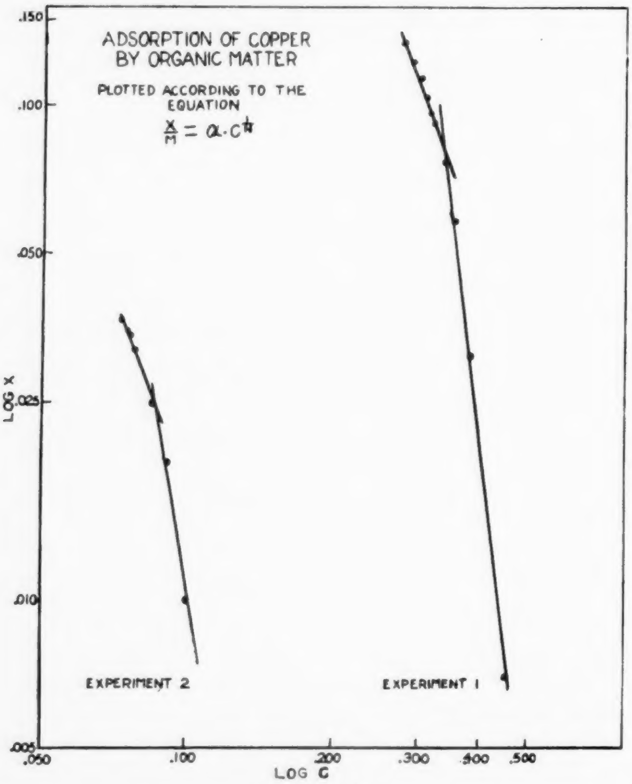

FIGURE 12

ratio, the partition coefficient (Nernst, 1923). This not very probable explanation of the phenomenon does not, however, alter the general conclusion that organic matter is responsible for the removal.

There is evidence that inorganic precipitation does not take place to a measurable degree:

1. Precipitation reactions do not obey the adsorption law.

2. A precipitate would settle out of the solution. This did not occur. A total copper test was made of the water from the first experiment four days after the initial addition of copper. The flask had not been disturbed for two days, and the water was pipetted from the upper part of the flask. The result was identical with the amount known to be present. It would have been less if precipitation had occurred.

Regeneration of Copper in the Lake Basin

It has been shown that certain variations of copper are of too great a magnitude to be explained on the basis of entrance of copper into the lake basin. One must therefore conclude that there are sources of copper within the basin which are at certain times available to the lake water and at such times greatly increase its copper content. The two possible sources are decaying littoral plants and lake mud. It is with the latter, a more general source throughout the year, that we are especially concerned here.

It is obvious that the detritus from dead plankton will accumulate copper, and as it sinks through the water the copper will be carried down with it. Decomposition of the detritus liberates some copper, for it will be recalled that the soluble copper develops a direct stratification during stagnation periods. But the preponderance of copper in the bottom waters is never as great as that of some other substances, such as iron and phosphate, which are carried down in much the same manner. It appears probable, therefore, that copper is easily removed from the lower part of the hypolimnion by sedimentation of organic detritus, and perhaps by adsorption on mud particles.

The mud at the bottom of the lake thus contains an abundance of copper, and experiments show that the mud can be a source of copper for the lake water. The method of testing regeneration was to make a ten per cent suspension of mud in distilled water, mix it thoroughly for several minutes, then filter out the mud and test the water for copper. In two sets of experiments the amount of copper available for regeneration ranged from 1.1 to 24.9 mg. of copper per liter of mud.

Regeneration may be regarded as two distinct processes. The first is the mechanical suspension of particles of mud containing copper. It is probably less important than the other because only the smallest particles can form a stable suspension. The second type involves the liberation of copper in ionic form. The tendency of mud to remove copper from the lower waters indicates that the equilibrium between ion and copper in combined form may be expressed as a mass action equation: copper adsorbed on mud $\rightleftarrows$ Cu ion, the reaction tending to go to completion toward the left. But according to the mass action law, the equilibrium will be shifted toward the right if copper ion is removed from the mud as fast as it is formed. This is what occurs when lake currents pass the water over the mud rapidly. The reaction between copper ion and organic matter in the lake is of the same type; consequently the expression may be expanded to: Cu adsorbed on mud $\rightleftarrows$ Cu ion $\rightleftarrows$ Cu adsorbed on organic matter in the lake water. The conclusion reached from these theoretical considerations is that the amount of regeneration bears a direct relationship both to the amount of mixing and to the quantity of organic matter in the lake, but the latter is dependent on the former, because the organic matter must be brought into contact with the mud in order to be effective as a regenerative agent, and the quantity which passes over the mud is dependent on the amount of mixing.

Conditions in the lake favor this hypothesis; therefore it was desirable to test it further by experiment. 30 cc. of mud were placed in the bottom of a suction flask. A tube extending into the mud carried water into the flask at a rate of 45 cc. per minute. The water gradually rose and overflowed through the side arm of the suction flask, where it was caught in another flask and analyzed.

The experiment was performed with two kinds of water: a membrane filtrate from Linsley, and the membrane filtrate mixed with some water of high organic content that had been collected during the autumn, the proportions being 4:1. Therefore the first sample may be regarded as lake water unusually low in organic matter, since the larger particles had been removed, and the second was moderately high. The copper content of the water was determined before and after contact with the mud, and the results of these analyses are shown in Table 7.

TABLE 7. REGENERATION OF COPPER FROM LAKE MUD.

Before treatment with mud:

	Filtered water	Filtered—unfiltered water
Total Cu	.033	.056
Soluble Cu	.014	.011
Seston Cu	.000	.010
Organic Cu	.019	.035

After treatment:

	Filtered water	Filtered—unfiltered water
Total Cu	.036	.070
Soluble Cu	.017	.012
Seston Cu	.001	.021
Organic Cu	.018	.037

Increment in copper during treatment with mud:

	Filtered water	Filtered—unfiltered water
Total Cu	.003	.014
Soluble Cu	.003	.001
Seston Cu	.001	.011
Organic Cu	—.001	.002

Thus, under these conditions, the amount of regenerated copper is greater when the particulate organic matter is high. Most of the copper goes into the seston fraction, the increase in soluble and organic copper being small but probably significant. When there is little particulate matter, the increase is slight and is largely in the soluble fraction. The increase due to mud suspension is hardly significant, .001 in this experiment, as shown by the increment in seston copper in the filtered sample.

These conditions are probably applicable to the natural conditions obtained in lakes. But in another experiment, in which the mud and water were mixed very thoroughly and allowed to remain in contact for several hours, the effect of organic matter was insignificant. It should therefore be added that if an overturn ever approaches completion (when all the copper is dissolved from the mud, and the copper in the lake is at adsorption equilibrium), the effect of organic matter on regeneration will approach zero.

Biological Action

(a) *Plankton.*

It is impossible to measure the amount of copper in living plankton because of the difficulty of separating it from detritus. But if it contains the same relative amount of copper as higher plants, the amount of copper in all the plankton would never exceed one kilo and would average less than 300 g. This amount is measurable but is insignificant in comparison to the usual amount of seston copper, and consequently the effect of plankton variations on the copper content of the lake may, from this standpoint, be regarded as negligible.

It is likely, however, that the plankton has an important indirect effect. The organic detritus in the lake is largely derived from the plankton. Therefore, since it appears that regeneration is partly controlled by the organic content of the lake, and since it is even more important for the sedimentation process, plankton production has a very real effect on copper variations.

Harvey (1937) has shown that large quantities of iron and phosphate become adsorbed on the surface of diatoms. It is quite possible that they remove copper in the same manner. The diatoms would therefore have the same effect as non-living particulate organic matter.

(b) *Littoral plants.*

A major difference between the plankton and littoral plants is the seasonal aspect of the latter. Consequently, the possible effects of littoral plants would be a decrease in the copper content of the lake during the spring and summer growing period and a corresponding increase in the autumn upon decomposition.

There are no available measurements of littoral plants in these lakes, but very rough estimates may be made from the work of other investigators. The amount of copper in plants averages about 20 mg. per kilo. The amount of littoral vegetation in Mendota is about 15,100 kilos per hectare (Rickett, 1920). The mean standing crop of plankton per unit volume in Mendota is comparable to that of Connecticut lakes, so that there should be no great error in the use of the Mendota figures. Basing the calculation on the area of the bottom above the five meter isobath, the amount of copper in littoral plants is about .9 kg. in Linsley, 8.2 in Quonnapaug, and 12.6 in Quassapaug. These estimates may be a little too low, for the amount of copper accumulated

is to some degree dependent on the quantity available in the soil, and the availability is high in a lake. Therefore it must be concluded that the copper in littoral plants is not a major factor in the autumn maximum, although it contributes to it slightly.

(c) *Effects of biological phenomena outside the lake basin.*

The autumnal decay of vegetation around the lake appears to be an important factor in the copper increase at that period. Annual plants contain copper in the usual amounts, generally not more than 40 mg. per kilo. The shed leaves of perennials are somewhat higher. Three analyses made in October, 1936, of oak, elm, and maple leaves show values ranging from 30 to 349 mg. per kilo. The copper in plants is evidently more readily available than that in the soil because during the period when the vegetation was dying most rapidly, from the first of October until the middle of November, 1936, the copper in the inlets was greater than in the surface water of Linsley, although the precipitation was larger than normal at that time. When there are heavy rains, and the water coming into the lake is largely surface drainage, it cannot have a very large quantity of copper in it unless there is a readily available source on the surface of the ground. Therefore, the simultaneous occurrence of dead plant remains and an exception to the general rule of dilution effects logically appear to show causal connection. Ground water may show the same effect to some extent, and leaves falling into the lake probably have some slight significance.

The effects of human habitation around these lakes are probably negligible. There are no industrial wastes in the basins and no large refuse heaps. Although the north inlet at Linsley, where one would expect the greatest amount of contamination, is usually a little higher than the other, the difference is more readily accounted for by adsorption of copper from the water of the southeast inlet by the large amount of organic matter in the swamp through which it passes.

Application of Copper Distribution Factors to the Stratification and Seasonal Cycle

(a) *Vertical distribution.*

Having evaluated, as far as possible, the factors which affect distribution and variation of copper in lakes, there are certain generalizations that may be made in explanation of the original data. In examining the vertical distribution it becomes evident that the two most important factors are regeneration and sedimentation, the latter being the adsorption of copper on organic particles as they sink through the water.

The reader is again referred to the graph of vertical distribution in Linsley, Figure 8, and the accompanying explanation. The irregularities in distribution at the time of the overturn are probably due to water currents passing over the mud and regenerating copper; since the circulation is seldom com-

plete enough in the lower water to distribute the suspension uniformly, the curve becomes highly irregular because of the errors of sampling a non-homogeneous mixture. This was more marked in some of the other overturns which were more complete (autumn overturns in all three lakes).

After the thermocline was established there was little mixing of hypolimnetic waters and no evidence of regeneration in that region. For the next few weeks sedimentation was clearly the dominant process and was responsible for the decrease in copper at the surface and the increase at lower levels. But although the hypolimnion was relatively stable during the summer months, and its characteristic behavior was a continuous sedimentation of the copper brought into it, the epilimnion, where mixing still took place freely, behaved in a more complex manner. There sedimentation and regeneration were opposing forces with the dominance frequently shifting from one to the other. This was responsible for the variety of curve types obtained during the summer and autumn months, pronounced regeneration in the epilimnion producing an inverse stratification, and sedimentation returning it to the direct type. And to some extent the two phenomena may occur simultaneously, the predominance varying at different levels, so that the curve is usually complex, a mixture of the two pure types.

Regeneration became especially marked after the middle of August; when the lake began to lose heat, mixing naturally occurred to successively greater depths, permitting regeneration from mud that had been relatively undisturbed throughout the summer. Although the currents are not so strong in the lower part of the lake, there is much more copper available in the hypolimnetic mud. During a stratification period continual sedimentation of copper-containing particles takes place. Those falling into the hypolimnetic mud remain there, while those in the epilimnion are stirred up and redistributed, part of them eventually falling into the hypolimnion. Thus a gradual preponderance of copper is built up in the lower part of the lake. This was clearly shown in some of the regeneration experiments, in which the available copper was found to be distinctly greater at the bottom than at two, or even eight, meters.

The copper adsorption experiments throw some light on the relations of the different fractions. Under natural conditions, i.e., in open water not in contact with mud or other sources of copper, it is probable that there is an adsorption equilibrium established, the position of the equilibrium shifting with variations in the amount of organic matter. The adsorbed copper is distributed between the seston and organic fractions, the variations of which tend to bear an inverse relation. This latter may be due to changes in size of the particles during decomposition.

According to the adsorption theory, when the organic matter is decreased, as by decomposition, the equilibrium shifts, and copper ion is liberated. In the first adsorption experiment the quantity of ion was .360 mg. per liter on the twelfth day, having risen .084 mg. from the lowest point of .276 mg.

recorded on the second day. Likewise in the lake, where decay is greatest in the bottom waters, there is always a tendency toward an increase in soluble copper, which results in direct stratification. Nevertheless, there are occasional sharp decreases of copper ion in the hypolimnion, which are probably due to adsorption on mud and particulate organic matter.

(b) *The seasonal cycle.*

It has been suggested, largely on theoretical grounds, that there are certain factors which influence copper distribution: namely, precipitation, littoral vegetation, the vegetation of the drainage basin, the quantity of organic matter in the lake water, and the rate of regeneration of copper from lake mud. It is evident that the final proof of the validity of these factors must rest upon a correlation of their seasonal aspects with the seasonal cycle of copper. The effects of precipitation and organic matter can be stated in numerical terms, but the other factors cannot be measured directly with any reasonable degree of accuracy, and it is therefore unfortunately necessary to substitute arbitrary indices.

Hutchinson (1938) has shown that throughout the summer stagnation period the alkalinity is increased by regeneration from the mud, and this appears to be the only major factor involved. It is assumed here that the regeneration of bicarbonates and of copper are similar processes and consequently that increases of copper caused by regeneration from the mud are proportional to alkalinity increments. Therefore the alkalinity is used as an index of regeneration.

The second major assumption is that the rate of decomposition of littoral vegetation in the autumn is greatest when the temperature of the upper five meters of lake water is decreasing most rapidly, and, conversely, the rate of growth in the spring is greatest when the temperature is increasing most rapidly. Therefore, increases in copper due to this factor are regarded as proportional to decreases in temperature during the same period.

It is also assumed that the liberation of copper from vegetation of the drainage basin follows the same temperature curve during the autumn and early winter months. But the two curves differ in that littoral plants extract copper from the lake water during the spring and summer, whereas the plants outside the lake basin presumably have no effect during this period. Therefore, increases in copper due to the vegetation of the drainage basin are proportional to decreases in temperature, but all negative values for the latter are raised to zero.

Having determined what appear to be the best possible indices of the various factors, we can proceed to analyze their effects on the copper cycle by means of multiple correlations. The method of Bruce and Reineke (1931) is employed for this purpose. The linear regression equation is calculated according to the formula

$$\mathrm{W} = W + \mathrm{Bwx}\frac{\sigma \mathrm{w}}{\sigma \mathrm{x}}(\mathrm{X} - X) + \mathrm{Bwy}\frac{\sigma \mathrm{w}}{\sigma \mathrm{y}}(\mathrm{Y} - Y) \qquad (1)$$

where W is the independent variable; X and Y are the dependent variables; *W, X, Y* are the means of the variables; σw, etc. are the standard deviations; and Bwx and Bwy are constants calculated from the correlations r_{wx}, r_{wy}, and r_{xy}. This type of equation can be extended indefinitely to include any desired number of dependent variables.

Thirty complete sets of data are available for the calculation of regression equations for Linsley. These include all but one of the analyses from Oct. 19, 1935 to Dec. 5, 1936. The necessary basic values derived from these data are shown in Tables 8 and 9.

TABLE 8. MEANS AND DEVIATIONS OF COPPER AND RELATED FACTORS.

	Symbol	Mean	σ
Copper	W	32.54	30.84
Alkalinity	X	45.25	4.92
Precipitation	X′	1.93	1.27
Organic matter	Y	2.27	1.08
Littoral vegetation	Z	.44	1.97
Basin vegetation	Z′	1.04	1.37

TABLE 9. COEFFICIENTS OF CORRELATION

	Symbol	W	X	X′	Y	Z
Means and Deviations of Copper and Related Factors	X	.541				
	X′	—.249	—.263			
	Y	.037	.437	—.012		
	Z	.536	.493	—.082	.315	
	Z′	.541	.497	—.096	.306	.962

The equation obtained when all factors are employed in the calculation is

$$W = 2.60X - 2.58X' - 8.24Y + 5.33Z + 2.34Z' - 63.94 \quad (2)$$

The correlation between the expected quantity of copper in the lake, calculated from the equation, and the actual amount is .696. It is exactly the same as the correlation obtained from the equation

$$W' = 1.82X - 3.18X' + .96Z + 7.25\,Z' - 51.74 \quad (3)$$

which includes all the factors except organic matter.

The relationships of these variables are not linear, and it is possible to increase the coefficients of correlation significantly by the application of curvilinear methods. The method developed by Bruce and Reineke is designed for problems such as this, in which the equations for the curves are unknown, and the final results are obtained by semi-graphical means. When their technique is applied to equation (2) the coefficient of correlation is raised to .821, and for equation (3) it is .839. The curves for the theoretical seasonal distribution of copper obtained by this method are shown in Figure 13 together with observed values.

The difference between the final correlations obtained from equations (2) and (3) is not significant. It therefore appears that the effect of organic matter is negligible, and this is also indicated by the fact that the original correlation between copper and organic matter is insignificantly small. But it was pointed out that organic matter plays a dual role; it assists both the sedimentation and regeneration of copper. It would appear that sedimentation is the more important phenomenon, since in equation (2) Y is negative. According to the theory outlined above, the effect of organic matter on the removal of copper from the water is most marked during periods of stagnation, but when mixing is extensive, as during an overturn, regeneration becomes a dominant process. If this is true, equation (2), which makes sedimentation dominant throughout, would provide a better fit for the original data during the summer stagnation period, but during an overturn it would give poorer results than equation (3), which ignores the effect of organic matter altogether. That such is the case is evident from Figure 13.

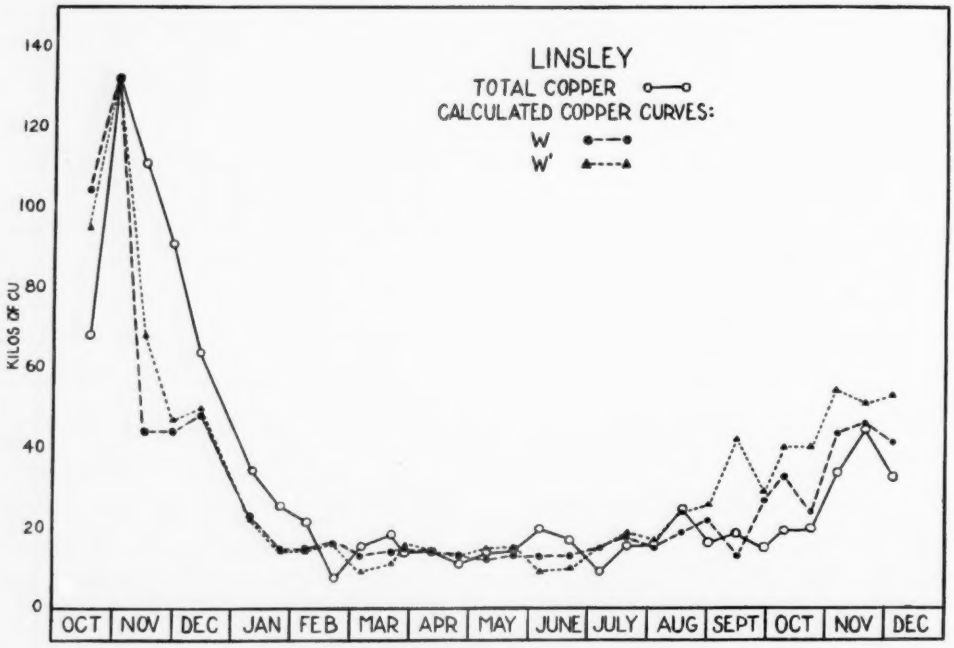

FIGURE 13

It would be interesting to evaluate the relative importance of the different factors, but this can be done only in the most general way. It is evident that the constants developed in a multiple correlation are not completely valid; they are merely statistically accurate for a given set of variables. Consequently, the introduction of additional variables changes all the constants, and the only statistical criterion of the validity of the procedure is the comparison of the coefficients of correlation. In this particular case there are several practical reasons for believing that equation (3) is better than (2), but it is not possible to make a statistical choice.

Furthermore, there are sampling errors involved which can change the equation considerably. For example, if the correlation between copper and alkalinity is changed from .541 to .454, the lower limit of the probable error, equation (3) is changed to

$$W' = 1.14X - 3.88X' + 3.15Z + 5.32Z' - 18.5$$

It may now be stated that according to equation (3) the relative importance of the factors, determined on the basis of the products of their constants and standard deviations, is as follows: $X : X' : Z : Z'$ as $55 : -23 : 11 : 57$. But according to the above qualifications, these ratios must be regarded only as rough approximations, and considering the possible influence of undiscovered factors, it is impossible to estimate the limits of variation.

Applying the same set of factors to Quonnapaug and Quassapaug, the following results are obtained:

Quonnapaug: $W = 3.14X - 2.74X' + 12.00Z - 8.15Z' - 165.6$ (4)

Quassapaug: $W = 36.3X + 147X' - 99.7Z + 204Z' - 4165$ (5)

The coefficient of correlation for Quonnapaug is .745 and for Quassapaug .591. It is reasonable to suppose that the value of Z' in the Quonnapaug equation and of X' and Z in Quassapaug might be insignificantly small. It is not reasonable that the signs should be reversed. Since the correlations are improved by the omission of these factors, it is probable that the reversal is due to errors involved in the use of insufficient data, for only sixteen sets of analyses were available for each lake. The corrected equations are as follows:

Quonnapaug: $W = 2.38X - 2.74X' + 7.77Z - 113.1$ (6)

Quassapaug: $W = 8.84X + 58.8Z' - 674$ (7)

The correlations are .774 and .690. They are not significantly improved by the use of the curvilinear technique.

These differences in the equations give a satisfactory explanation of the difference in the form of the seasonal cycle in the three lakes. It is to be expected that the effect of precipitation would be slight in Quassapaug because the ratio of lake area to drainage basin area is large. Furthermore the littoral vegetation appears to be scanty except in the shallow bays. In Quonnapaug, on the other hand, the effect of littoral vegetation is greater than in either of the other two lakes because its mean depth is less and also because its inlet is derived from a large, shallow pond, which, from this standpoint, is virtually an extension of the littoral zone of the lake itself.

COPPER TOLERANCE EXPERIMENTS

The study of the toxic effects of copper began in 1881, when Richet, experimenting with the Mediterranean fishes *Serranus* and *Crenolabrus*, reported that there is no relation between the atomic weight of a cation and its toxic effect, and that the greatest amount of copper tolerated by these genera is 3.3 mg. per liter. Nägeli (1893) obtained the same type of results with

two species of *Spirogyra* and coined the term "oligodynamic" to express the toxic action of small quantities of certain metallic ions. During the next few years it was shown that the oligodynamic action could be applied to all groups of organisms (Bekorney, 1896; Ono, 1900; Devaux, 1901; Coupin, 1901; Bain, 1902; and Moore and Kellerman, 1904-5). The last two authors are especially important because of their development of a method for the removal of undesirable micro-organisms from reservoirs by treatment with copper sulfate. Their method was further refined by Hale in 1922.

Powers (1917), working on the goldfish, *Carassius carassius,* showed that the survival curve in different concentrations of a metallic ion breaks sharply. The form of the curve superficially resembled a hyperbola.

Carpenter (1927, 1930) found that the toxic action of heavy metal salts in fishes is due to an impediment of respiration by the formation of a film of coagulated mucus over the gills. She suggested that the survival curve has an exponential form.

According to Jones (1935), who used the three-spined stickleback, *Gastrosteus aculeatus,* for his experiments, the toxic action of heavy metal salts is due exclusively to the cation in hypotonic solutions. Nevertheless, different salts of the same metal have slightly different degrees of toxicity which are proportional to the product of the cation and the electrical conductivity—i.e., to the ionization—of the salt.

The work of Moore, Kellerman, and Hale provides abundant evidence on the toxicity levels of freshwater algae and protozoa. The experiments on invertebrate metozoa, on the other hand, are few in number and incomplete. Before attempting to evaluate the ecological significance of copper it was therefore necessary to determine the tolerance level of representatives of the invertebrate groups that are important in the freshwater biocoenosis.

Material and Methods

Ten types of organisms were used for the experiments: one protozoan, one coelenterate, one rotifer, two copepods, three cladocera, and two insect larvae. In three experiments—*Daphnia magna, Ceriodaphnia quadrangulata,* and *Epistylis plicatalis*—the animals were grown in the laboratory with each group derived from a single individual. The other animals, difficult to rear under laboratory conditions, were taken from lakes or ponds and selected so as to correspond as nearly as possible in size and development.

The basic medium in all experiments was natural water from the place in which the animals had been found, or the same kind in which they had been cultured in the laboratory. The general procedure was to place 190 cc. of lake water in a finger bowl, introduce the animals, and then add 10 cc. of distilled water containing the desired amount of copper. In the first few experiments 50 cc. of water were used, but it was not enough for the larger or more rapidly moving animals.

Generally five animals were put in each dish, occasionally more, and in two experiments only two. It is definitely not desirable to use fewer than five animals. But in these cases the animals were scarce, and it was important to get some data for them, even though it was faulty from the quantitative standpoint. Statistically it would have been better to use more than five animals in each dish, but practically it is better not to. Each animal must be examined frequently with the microscope to determine the time of its death, which limits the number of animals that can be studied simultaneously without endangering the accuracy of the time record.

An important part of the experiment is the decision as to the proper criterion of the death of an animal. It is best to choose some movement that is constant and habitual, such as ciliary motion, heart-beat, or respiratory rhythms. When more than one of these were available, the one that ceases last was selected. In some cases none of these movements occurred, and it was necessary to resort to other means. For example, in *Hydra* the cessation of the contraction response to touching with a glass needle was used as the criterion of the death point.

Discussion

(a) *Toxicity of copper and pathological effects.*

The results of the toxicity experiments are shown in Table 10.

It appears generally true that copper has a toxic effect only when it enters the tissues of an animal, although there are certain general exceptions, such as that noted by Carpenter (1927, 1930) in which the copper formed a coagulated film of mucus over the gills of fishes, which impeded respiration.

If the general rule holds good, susceptibility to copper poisoning is a function of the permeability of the integument. Various toxic substances behave in this way, as shown by Alexandrov (1935) in his ingenious experiments with the chitin of dipterous larvae. One of his most impermeable animals, *Chaoborus,* is exceedingly resistant to copper poisoning, and the magnesium tolerance of Cladocera (Hutchinson, 1932) appears to be somewhat similar to their copper tolerance. Furthermore, in *Daphnia magna* killed by copper, there are sufficient quantities of the element in the intestine, heart, and muscles to be detected by a brown stain in these organs when the animals are immersed in a solution of the copper reagent, sodium diethyldithiocarbamate.

The pathological effects of copper are quite heterogeneous, but they have certain general characteristics that are common to most or all of the animals studied: There is first a stimulation of movement, which appears to be caused by general irritation. This is followed by the toxic effect, which slows down the vital mechanism and leads eventually to death, and is accompanied by degenerative morphological changes.

TABLE 10. COPPER TOXICITY EXPERIMENTS.

Survival time in hours.

Concentration of copper in mg./l.	*Epistylis plicatalis*	*Hydra* sp	*Hydra* sp	*Conochilus hippocrepis*	*Ceriodaphnia quadrangulata*	*Daphnia pulex*	*Daphnia magna*	*Mesocyclops edax*	*Tanypus* sp	*Chaoborus punctipennis*	*Diaptomus spatulocrenatus*
200	....	....	....	....	....	....	....	....	....	124	....
50	4.0	.17	....	.73	....	.63	....	3.8	24.6	216	....
40	....	....	....	....	.93	....	4.05	....	....	....	.45
20	4.5	.17	....	....	.97	.83	....	6.5	30.6	....	.52
10	4.7	.19	....	1.03	1.38	.83	5.37	105	35.2	259	.67
1.0	13	.27	.9	1.28	2.08	1.12	6.35	382	89.0	175	.75
0.5	18	.27	3.1	1.33	2.97	1.15	6.60	636	106	601	.80
0.2	....	....	....	1.07	....	....	....	474	....	347	....
0.1	....	....	....	2.16	....	....	30.0	624	....	482	....
0.05	44	1.5	4.7	2.25	4.10	1.63	40.6	—	....	139	.14
0.03	....	....	17	....	....	7.00	76.0	....	....	....	....
0.01	—	2.5	—	2.30	—	—	—	—	....	134	—

— A dash indicates that the animals were in good condition at the end of the experiment. The death of the controls in the experiments with Conochilus and Hydra indicates that the animals were in bad condition at the beginning of the experiment, and the curves are therefore not completely valid. Death of the Chaoborus controls was probably due to starvation, and intermediate concentrations of copper inhibited this effect by slowing down the movements of the animals.

(b) *Copper tolerance curves.*

Curves obtained by plotting the concentration of copper against the period of survival are shown in Figure 14. The curves break very sharply, especially when the animal is very susceptible to copper poisoning. Above the break the decrease in the survival period is very slight compared with the increase in concentration.

This is the same type of curve as those obtained by Powers (1917, 1920), who pointed out their resemblance to hyperbolas. But in each of these experiments the values of the constant, obtained according to the usual equation, $a = xy$, vary several hundred per cent. The resemblance is therefore superficial and depends on the form of the curve, which minimizes small variations in time on one axis, and in copper concentration on the other.

Carpenter (1927) obtained data which did not bear any resemblance to hyperbolic curves but could be fitted by an exponential equation

$$K = \frac{1}{t} \log \frac{1}{\text{conc.}} \cdot$$

In order to test this hypothesis I plotted log 1/concentration against 1/t for several of the experiments. But instead of a straight line, two lines were obtained (Figure 15).

The data fit the curves about as well as in Carpenter's experiments. The only one which could possibly be fitted by a single straight line is that with Tanypus. Since she used high concentrations of metallic salts (.005 — .2 N), the question arises as to whether or not her experiments with minnows would

have shown a break in the curve at lower concentrations. Powers used about the same concentrations as Carpenter and obtained curves similar to mine, but he worked with the goldfish, which is a more resistant animal. Therefore it is quite possible that the curves for minnows would have taken this form if the concentration of copper had been less. In one experiment, with lead nitrate in a small volume of medium, there was a divergence from the theoretical curve in low concentrations. But Carpenter pointed out that this was due to removal of lead from solution by the gills of the fish rather than a change in the type of toxicity reaction.

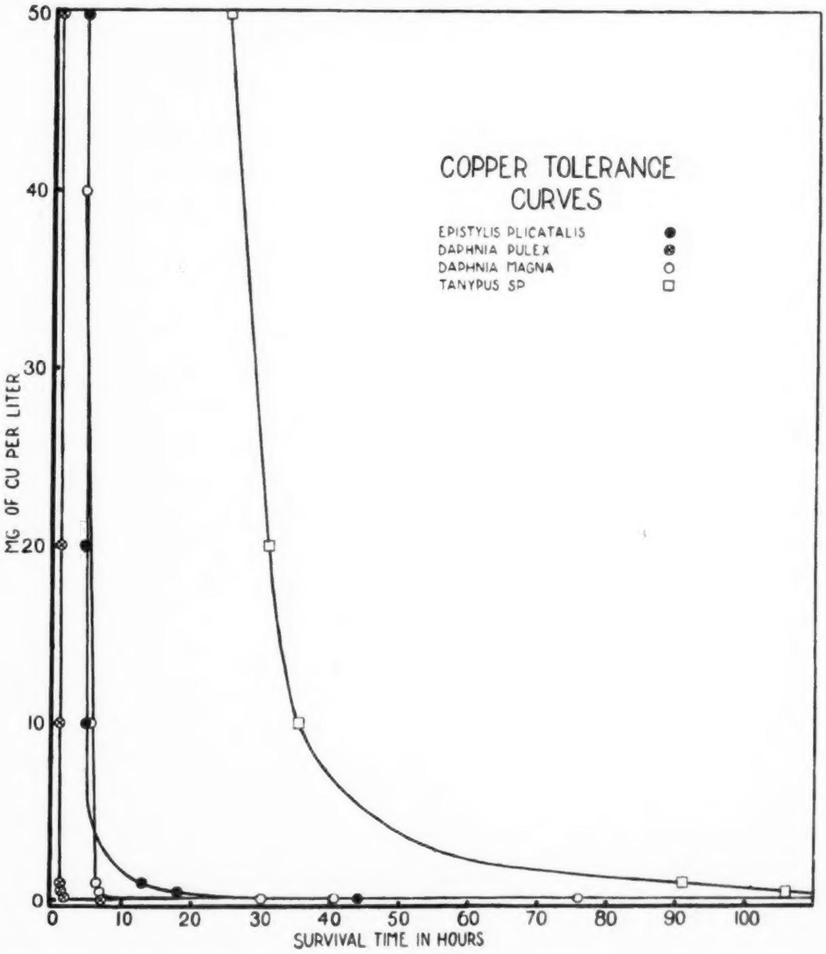

FIGURE 14

My experiments, designed chiefly for ecological purposes rather than a study of the physiology of copper poisoning, are hardly complete enough to warrant a final statement in the matter. But it is quite possible that the apparent inconsistency between the results of the two previous workers can be explained by assuming that the constants of the toxicity reaction are not the same at all concentrations.

Biology

The results of the study permit certain general conclusions in regard to the biological significance of copper in lakes. In the first place, since there is always copper in these waters in some form, and since very little is required by animals and plants, it cannot be regarded as a limiting factor from the standpoint of deficiency. But it is at certain times of the year high enough to have a possible ecological significance by its toxic effect.

The older workers showed that the toxicity threshold varies widely in different animals and plants. Some forms can tolerate from one to ten milligrams or more of copper per liter, and these animals would never be affected by copper in natural waters of the ordinary sort. On the other hand there are some organisms that cannot tolerate the quantity of copper found at certain times in Connecticut lakes. According to Hale's figures (1922) *Coelastrum, Navicula,* and *Euroglenopsis* belong in this class, and *Anabaena, Aphanizomenon, Tabellaria,* and *Synura* are borderline cases which might be affected during years when the copper is unusually high.

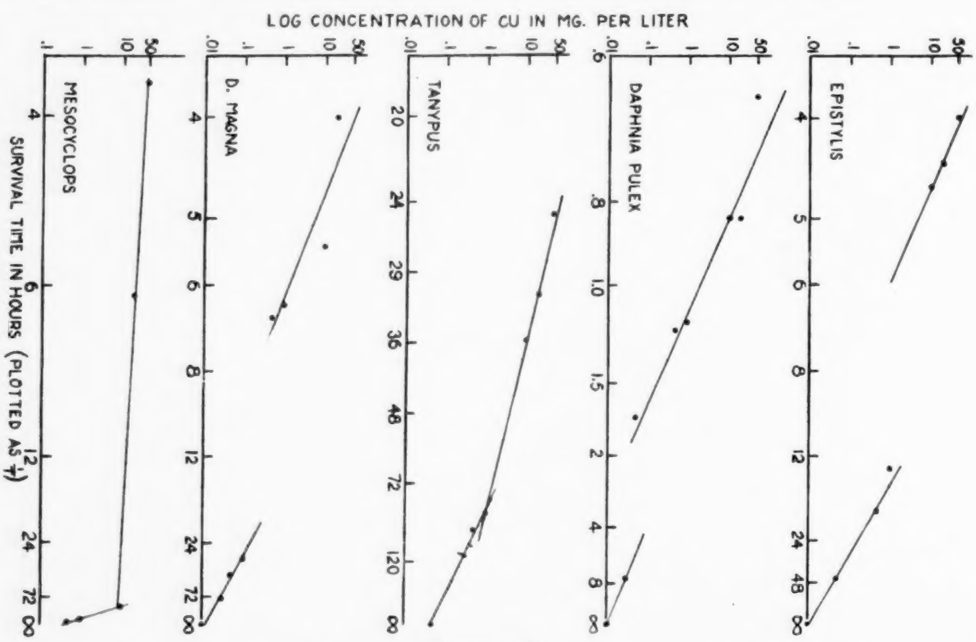

Figure 15

About half the animals in my experiments were unable to survive a concentration of .030 mg. per liter, which is not unusually high for lake waters in the autumn. This is true of *Hydra, Conochilus, Daphnia pulex,* and perhaps *Ceriodaphnia* and some Diaptomids.

Results of this sort indicate that there are probably many animals within the same tolerance range. It may therefore be stated provisionally that copper is important from the ecological standpoint, although there are certain complicating factors that tend to rob it of its significance.

First, the time when the copper is highest is the autumn, when other factors in the lake are also inimical: rapidly falling temperature, and extreme stagnation in the bottom waters with low oxygen and high H_2S, iron, etc. Thus when a particular animal, e.g. *Hydra*, disappears from the lake at this time of the year, it is impossible to ascribe it definitely to copper toxicity. In the hypolimnion throughout the summer stagnation period the copper is higher than at the surface and is usually high enough to kill the more delicate animals that might wander into it from the littoral zone; but here again there is a complex of unfavorable factors. It is important to note, however, that the normal inhabitants of the hypolimnion are in general more tolerant to copper than littoral animals.

Second, the copper ion rises fairly slowly, so that there is sufficient time for an organism with low tolerance to copper to develop resting stages, or perhaps to become acclimated. The greatest rises in copper are in the combined fractions, and most of the forms are unaffected by these. But they might well be important to detritus feeders. For example *Daphnia pulex*, an animal with low tolerance to copper, is most common in Quassapaug, where the copper is lowest, and in Linsley, which has the greatest amount, it was found only once, and that was in the spring at a time when the copper was quite low. Also, in Quassapaug it declined considerably during the autumn months. But here again it is impossible to draw definite conclusions because of the difficulty of analyzing all the factors in an uncontrolled environment.

Finally, the toxic effect of copper is never quite as universally virulent as might be the case of a substance that is toxic in larger quantities because when it kills an organism it is automatically eliminating itself. It is so readily adsorbed on organic detritus that when it increases the amount of detritus by its toxic action, it is rapidly removed from solution, and the concentration of copper ion is lowered within a few hours to a non-poisonous level.

SUMMARY

1. Three Connecticut lakes were chosen for the investigation: Linsley, Quonnapaug, and Quassapaug. The limnological survey included measurements of temperature, color, hydrogen-ion concentration, alkalinity, oxygen, and the weight and chlorophyll content of the plankton.

2. Since a comprehensive investigation of Connecticut lakes had not previously been made, certain parts of the study were necessary for regional limnological purposes. These include temperature and the calculation of heat budgets, direct work curves, and stability; and pH, alkalinity, color, transparency, oxygen deficits, and plankton studies.

3. The remainder of the work is concerned with the interaction of environment and biota:

(a) Variations in transparency bear an inverse relationship to both color and the amount of plankton, and in a given lake the plankton is more important than humus color in causing variations in transparency.

(b) The oxygen deficit is not a satisfactory index of the productivity of shallow lakes. The ratio of deficit to organic matter is less than in deeper lakes, and this is due largely to photosynthesis in the hypolimnion.

(c) Neither chlorophyll nor total organic matter shows a bimodal seasonal curve. The amount of phytoplankton, estimated on the basis of the relationship between chlorophyll and organic matter, is not more than about one-fourth of the seston weight.

4. Determinations were made of total, soluble, seston, and organic copper. Analyses of the three lakes show no essential differences in total copper content, vertical distribution, or seasonal cycle.

5. The vertical distribution of total copper may be direct, inverse, or dichotomous, depending on the relative predominance at different levels of the two opposing processes, sedimentation and regeneration. Soluble copper shows direct stratification during stagnation periods; the seston and organic fractions are highly variable and tend toward an inverse relationship.

6. The total amount of copper in the lake is lowest in the middle or latter part of the winter. It tends to rise slightly at the time of the spring overturn but remains fairly low throughout the spring months, then gradually increases during the summer and early autumn. In October or November the copper rises sharply to the highest point of the year, following which there is a steady decrease to the minimum point in February or March.

7. By means of a series of multiple correlations it is shown that there are at least five factors which affect the copper content of lake waters: (a) precipitation, which lowers the copper content by dilution; (b) sedimentation, the removal of copper from solution by adsorption on organic matter; (c) regeneration from the mud; (d) liberation of copper from littoral plants in the autumn when they die and decompose, and removal of copper from the water during the growing season; (e) liberation of copper in the autumn by the decomposition of vegetation surrounding the lake. Slight differences in the form of the seasonal cycle in the three lakes are evaluated on the basis of differences in the relative influence of these factors.

8. The copper in lakes is never low enough to be an ecologically significant factor from the deficiency standpoint. During the autumn it is high enough to be toxic to some animals and plants; this is also true to some extent of the lower part of the hypolimnion throughout the summer. It is thus one of the complex of unfavorable factors which becomes ecologically important during the latter part of the summer stagnation period. During the rest of the year copper has no biological significance in these lakes.

9. The tolerance level of ten representative freshwater invertebrates was found to range from .03 mg. of copper per liter to more than .5 mg. The two animals with the highest tolerance were hypolimnetic forms.

10. The toxicity curve obtained by plotting concentration of copper against survival time superficially resembles a hyperbola; when plotted according to Carpenter's exponential equation, the curve is broken into two straight lines with different values for the constant.

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A LIMNOLOGICAL STUDY OF LAKE WASHINGTON

By

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CONTENTS

Fig. 1. Lake Washington from Laurelhurst.

A LIMNOLOGICAL STUDY OF LAKE WASHINGTON

INTRODUCTION

Historical

At present there is a meager limnological literature pertaining to the lakes of the Pacific Northwest. In 1911-1913 Kemmerer, Bovard and Boorman (1923) made a general survey of many northwestern lakes (including Lake Washington) in the interest of the U. S. Bureau of Fisheries. The wide scope of their project limited the study of each lake to a single series of chemical and plankton observations, though at the time they recognized the desirability of more extensive studies. Twelve years later the flushing of Lake Washington Ship Canal, connecting Lake Washington with Puget Sound, was studied by chemical methods, first by Smith and Thompson (1925, 1927) and shortly thereafter by Tilley, Semb and Thompson (1928). An ecological study has never been made of Lake Washington, though recently Scheffer (1933) made such a study of Echo Lake, near Seattle. The latter, though possessing characteristics of scores of shallow glacial lakes of this vicinity, can scarcely be compared with a large body such as Lake

Washington. Then too, certain limnological investigations have been made by Juday, Rich, Kemmerer and Mann (1932) on Karluk Lake, Kodiak Island, Alaska, because of its bearing on the salmon industry. In respect to its plankton, Karluk, an oligotrophic lake, has many features in common with Lake Washington, but is dissimilar in its chemical characteristics and climatic environment. Therefore, in view of this limited literature on the northwestern lakes a thorough biological and chemical survey of Lake Washington seemed desirable.

Physiography of the Region

Lake Washington, which owes its origin to combined glacial and river action, (Coombs 1938) has waters that have been slowly converted from salt to fresh. The lake bounds Seattle on the east, and is surrounded by rolling country terminating two to five miles westward in Puget Sound and fifty miles eastward in the Cascade Mountains. Lake Washington forms the drainage basin for 182 sq. mi. of territory, with an average annual precipitation of about 33.38 inches. It is fed by two main streams and several smaller tributaries. The Sammamish Slough, originating in Lake Sammamish several miles to the east, flows into the northmost end of Lake Washington, while the Cedar River, fed by melting snow in the Cascades, flows into the southmost end of the lake. Before the Lake Washington Ship Canal was constructed, water flowed from Lake Washington into the old Black River, was joined by the Cedar River, and then emptied into the Duwamish River. But with the completion of the canal in 1916 the level of the lake was lowered ten feet with subsequent diversion of the Cedar River into Lake Washington. Now the only outlet is through the canal into Lake Union and thence into Puget Sound. On account of the greater density of sea water a certain amount of salt water flows during lockages to the bottom of Lake Union, but cannot rise high enough to continue into Lake Washington. The normal elevation of Lake Washington is 21 feet above mean lower low water in Puget Sound.

Lake Washington is trough-like in shape, being 22 miles in length (air-line from end to end) and 1 to 4 miles in width, with an area of about 50 sq. mi. (128 square kilometers). It is barely exceeded in area by Lake Chelan, the largest lake in the state of Washington, with an area of 51 sq. mi. The U. S. Coast and Geodetic Survey Chart shows a maximum depth of 214 ft. (65 m.) for Lake Washington. The deepest part of the lake is in the central portion; it gradually shoals toward each end. The volume of the lake is calculated to be 3.14 x 10^9 cubic meters distributed as follows: 0-10 meters 28.2%, 10-20 meters 24.2%, 20-30 meters 20.5%, 30-40 meters 14.0%, 40-50 meters 8.8%, 50-60 meters 4.3%. The weighted average depth is then 18 meters.

Methods of Sampling and Analysis

All samples were collected from the M. S. Catalyst, research boat of the Oceanographic Laboratories. Samples were taken every three weeks throughout the period January 14, 1933 to January 20, 1934 from three stations selected as being representative of the lake. The Madison Park station, with a depth of 60 meters, was at the deepest and most central point of the lake. The North Point and South Point stations, each with a depth of 30 meters, were in the two ends of the lake and were considered typical of the shoaler waters.

The water samples for chemical analysis were collected in sampling bottles of the Nansen type to which were attached Richter-Wiese reversing thermometers for securing the water temperatures. The convenient Hellige pH comparator was utilized in measuring the hydrogen-ion concentration of the water. "Free carbon dioxide" and "bound carbon dioxide" were titrated according to methods of Seyler (1894). Winkler's (1888) well-known procedure was used for the determination of dissolved oxygen. The Denigés (1921) colorimetric method for soluble phosphate, Robinson and Kemmerer's (1930) method for organic phosphorus and Dienert and Wandenbulcke's (1923) method for soluble silicate as modified by Robinson and Kemmerer (1930b) were used for these determinations. Ammonia, after distillation, was estimated with the Nessler reagent, as was the Kjeldahl nitrogen as used by Robinson and Kemmerer (1930a). The phenoldisulfonic acid method for nitrate and the permanganate method for oxygen consumed were both used as described by the American Public Health Association.

The chemical data for only the Madison Park station have been included in this report because of the voluminous nature of the data and because the results from the other two stations were found to be essentially the same as at this location. In general the only difference was that the water at the other two stations was somewhat warmer and had a correspondingly earlier growth of plankton. Though all the data from the Madison Park station have been used in the construction of the graphs to show the seasonal variation, only those data for February 22 and August 19 have been included in tabular form in this report, Tables 1 and 2.

These two sets of data were selected as illustrative of the lake during the extremes of climatic conditions. For those persons desiring more detailed information of the lake than may be gathered from this report the complete record of chemical data for the three stations of Lake Washington has been filed by Robinson (1938) in the University of Washington Library.

All plankton samples were taken with a large closing net of the Hensen type designed to capture the net plankton but not the nannoplankton. The net was 220 cm. long with an intake opening 20 cm. in diameter. The net fabric was of No. 20 bolting silk with 50 meshes per cm., or 127 per inch. Hauls were made vertically, using the power winch of the M.S. Catalyst. A ver-

tical column of water extending from the surface to a depth of 30 meters (thus reaching almost to the bottom) was filtered at the two shallower end stations on the lake. At Madison Park, where the water is 63 meters deep, an additional column was filtered between the 60 and 30 meter levels. A 30 meter column, filtered with a net of this size having an estimated coefficient of filtration of 80%, represents about 750 liters, or 0.75 cu. m. of water. Workers in the field of planktology will understand the difficulty of measuring precisely the amount of water filtered by a net (Ricker 1932).

In determining the weight of a plankton sample the preservative liquid was removed by filtering through a Whatman No. 41 paper. After being dried and weighed, the filtrate was ignited in a porcelain crucible, as a means of determining the proportion of residual ash. Duplicate samples were taken for the purpose of enumerating the plankton organisms. Crustaceans were counted directly in a Rafter cell. For the smaller organisms an expression of relative frequency was determined by tallying the per cent of low-power microscopic fields, out of 200 surveyed, in which each species appeared. It was found that values ranged from 100% for certain diatoms during their maxima to 1% for the rarer algae, protozoans, and rotifers. Relative frequencies obtained by this method have been expressed as follows: (See Fig. 15.)

Appearing in 60-100% of the fields..........abundant
Appearing in 30-60 % of the fields..........very common
Appearing in 5-30 % of the fields..........common
Appearing in 1-5 % of the fields..........occasional
Appearing in less than 1% of the fields..........rare

TABLE 1. PHYSICAL AND CHEMICAL CHARACTERISTICS OF LAKE WASHINGTON AT MADISON PARK, FEBRUARY 22, 1933.

Depth	Temp.	pH	Carbon Dioxide		Oxygen		Phosphorus	
meters	°C.		Free mg./l.	Bound mg./l.	mg./l.	% Sat.	Soluble mg./l.	Organic mg./l.
0	5.42	7.50	+2.50	12.00	10.55	83.5	0.007	0.010
5	5.36	7.50	2.00	12.00	10.26	81.0	.007	.016
15	5.35	7.50	2.15	11.20	10.55	83.5	.007	.011
30	5.34	7.50	2.35	12.00	10.55	83.5	.007	.013
45	5.36	7.50	2.00	12.75	10.78	85.0	.007	.010
62	5.34	7.50	2.00	12.50	11.08	87.0	.007	.007

Depth	Silicon	Chloride	Nitrogen				Oxygen Demand
meters	mg./l.	mg./l.	NH_3-N mg./l.	Org.-N mg./l.	NO_3-N mg./l.	NO_2-N mg./l.	mg./l.
0	2.8	1.70	0.010	0.11	0.10	0.000	2.25
5	2.8	....	....	....	.09	.000	....
15	3.0	1.65	....	....	.12	.000	....
30	3.0	1.85	.008	.11	.10	.000	2.17
45	2.8	1.90	....	....	.09	.000	....
62	2.8	1.85	.010	.09	.12	.000	2.17

TABLE 2. PHYSICAL AND CHEMICAL CHARACTERISTICS OF LAKE WASHINGTON AT MADISON PARK, AUGUST 19, 1933.

Depth	Temp.	pH	Carbon Dioxide		Oxygen		Phosphorus	
			Free	Bound			Soluble	Organic
meters	°C.		mg./l.	mg./l.	mg./l.	% Sat.	mg./l.	mg./l.
0	21.85	7.80	+0.70	....	8.58	97.0	0.000	0.010
5	21.80	7.80	.90	....	8.67	98.0	.000	.013
10	19.34	7.50	1.30	....	8.74	94.0	.000	.013
12	16.71	7.30	2.10	....	8.13	83.0	....	....
13	13.14	7.35	....	....	8.04	76.0	....	....
14	12.30	7.25	....	....	8.27	76.0	....	....
15	11.15	7.25	3.10	....	8.32	75.0	.000	.013
18	9.96	7.25	3.20	....	8.81	78.0	....	....
20	9.38	7.25	2.80	....	9.04	79.0	.000	.013
30	8.04	7.25	3.30	....	9.20	77.5	.003	.011
40	7.21	7.10	3.70	....	9.05	75.0	.009	.008
50	6.76	7.10	5.10	....	8.12	66.0	.013	.002
60	6.62	6.90	6.10	....	6.36	52.0	.017	.005

Depth	Silicon	Chloride	Nitrogen				Oxygen Demand
			NH_3-N	Org.-N	NO_3-N	NO_2-N	
meters	mg./l.	mg./l.	mg./l.	mg./l.	mg./l.	mg./l.	mg./l.
0	1.6	....	....	....	0.03	....	....
5	1.8	....	....	....	.03	....	....
10	1.8	....	....	....	.03	....	....
12	1.6	....	....	....	....	....	....
13	2.0	....	....	....	....	....	....
14	2.0	....	....	....	....	....	....
15	2.2	....	....	....	.03	....	....
18	2.2	....	....	....	....	....	....
20	2.8	....	....	....	.04	....	....
30	3.0	....	....	....	.04	....	....
40	3.4	....	....	....	.05	....	....
50	3.6	....	....	....	.04	....	....
60	....	....	....	....	.03	....	....

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PHYSICAL AND CHEMICAL CHARACTERISTICS OF THE WATER

TEMPERATURE AND WATER CIRCULATION

The temperature of lake water is closely related to air temperature and hours of sunshine. Birge and Juday (1914) have shown that the tempera-

ture of a lake is remarkably constant from one year to another provided the comparison is made for corresponding seasons. The following observations for Lake Washington should be quite characteristic, for, fortunately, 1933 was an average year throughout in respect to air temperature, rainfall and hours of sunshine, excepting a slightly subnormal air temperature in February and an excess of 9.7 inches of rainfall in December (U. S. Weather Bureau 1936).

The relationship between *air temperature, hours of sunshine,* and *water temperature* is shown in Fig. 2. Only those water temperatures for Madison Park showing an appreciable change of temperature with depth have been plotted. This graph brings out some interesting facts pertaining to the circulation of the lake. At the time the first samples were taken the temperature of the surface water was slightly less than that at 60 meters. That is, the density of the surface water was slightly greater than at the bottom. This naturally was an unstable equilibrium which resulted in an immediate interchange and mixing of the water column. During February and March the temperatures of the surface and bottom waters were almost identical, so that mixing by wind action was still extremely easy. Beginning in March the water began to warm and by June 21 a thermocline had formed between the 5 and 10 meter levels. Later in the season the thermocline was located between 12 and 15 meters. By October, it had entirely disappeared.

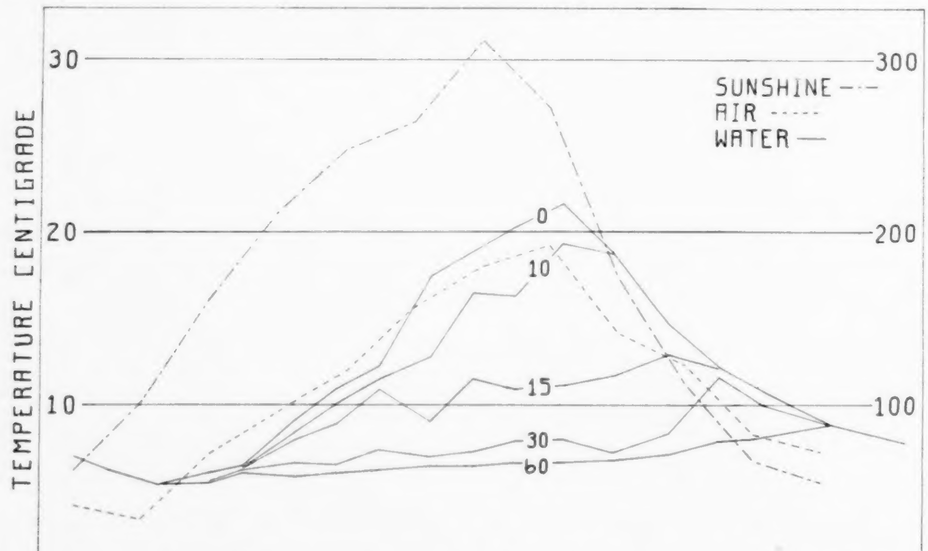

FIG. 2. Seasonal Variation of Air Temperature, Hours of Sunshine and Water Temperature.

A *maximum temperature* for the year of 21.85° C. was noted in the surface waters at Madison Park during the month of August. Kemmerer found 21.4° C. in August, 1913. Shortly thereafter the air temperature began to decrease and the water temperature also. The epilimnion increased

in thickness and by December the surface temperature was again almost identical with that of the bottom waters. The annual vertical circulation of the lake had thus begun and was to continue for a period of three months. It was during this period (in the month of February), that the *minimum surface temperature* of 5.42° C. occurred at Madison Park. Lake Washington thus had only one period of vertical circulation, though to be sure a long one, in contrast with the two shorter periods of lakes which freeze during the winter.

The *minimum mean temperature* of the lake was determined, as was also the *maximum mean temperature*. The minimum temperature occurred in February for 1933 and the maximum in August. The method of calculation was that used by Birge and Juday (1914), that is, the fraction of the total volume of the lake for a given water layer was multiplied by the average temperature for that layer. The sum of these results is the mean temperature of the entire layer. The calculations for Lake Washington are shown in Table 3.

TABLE 3. CALCULATION OF THE MINIMUM AND MAXIMUM TEMPERATURES OF THE WATER.

Depth	Fraction of Total Volume	February Temperature	(V) (T)	August Temperature	(V) (T)
0-10	0.282	5.77	1.62	21.17	5.96
10-20	.242	5.35	1.29	12.06	2.92
20-30	.205	5.34	1.10	8.71	1.79
30-40	.140	5.35	0.75	7.62	1.07
40-50	.088	5.35	.47	6.99	0.62
50-60	.043	5.35	.23	6.69	.29
			5.46°C.		12.65°C

The *annual heat budget* of the lake may readily be calculated from these data. The difference between the two mean temperatures multiplied by the mean depth of the lake in centimeters gives the heat budget expressed as gram calories per square centimeter of surface. Birge and Juday (1914) have admitted that no great accuracy can be claimed for the heat budget calculated in this manner but they maintain that the order of magnitude is correct. By this method of calculation Lake Washington was found to have acquired 43,000 gram cal. per sq. cm. of surface during the year 1933. In Table 4 a comparison is made of the heat budget of Lake Washington with those of certain European and American lakes (Birge and Juday 1915).

Birge has shown that some eastern American lakes have heat budgets of 35,000 to 39,000 gram calories. The European lakes seldom have more than 25,000 gram calories, though Lake Geneva has a mean heat budget of 36,600 gram calories. The heat budget of Lake Washington for 1933 was somewhat greater than, though of the same order of magnitude as, the eastern American lakes. This is due first, to the lesser mean depth of Lake

Washington, and second, to the fact that none of the insolation in early spring is expended in the melting of ice. It is interesting to note that 60% of the year's heat supply stayed in the first ten meters of water, roughly the epilimnion; 12% between 10 and 15 meters, the thermocline; and only 28% penetrated to the hypolimnion.

TABLE 4. ANNUAL HEAT BUDGET OF CERTAIN EUROPEAN AND AMERICAN LAKES.

Lake	Location	Mean Depth Meters	Cal. per Sq. Cm.
Washington	Washington	18	43,000
Geneva	France-Switzerland	154	36,600
Owasco	New York	29	35,000
Green	Wisconsin	33	34,000
Lochy	Scotland	70	31,500
Orta	Italy	71	25,400
Worth	Austria	43	25,300
Wurm	Germany	54	20,700

DISSOLVED SOLIDS AND CHLORIDE

The *dissolved solid* content was determined by weighing the residue after evaporation of the water sample at a temperature of about 60° C. Surface water collected January 28, 1933, contained 56 mg. per liter, and the water at 60 meters 66.5 mg.

The *chloride* content was so scant that it could not be determined accurately by the method given in "Standard Methods of Water Analysis," and the determination was therefore discontinued. For the one series of samples analyzed, the chloride content varied between 1.8 and 2.0 mg. per liter.

DISSOLVED GASES AND HYDROGEN-ION CONCENTRATION

All the gases of the atmosphere may be present in lake water, as well as those formed through decomposition of organic material. Only those which are of prime biological importance, *oxygen* and *carbon dioxide* have been investigated in this lake. Because of the direct correlation of *pH* to the free carbon dioxide content, it, too, has been included in the discussion of this grouping.

The total carbon dioxide content of lake water is usually divided into three groups for discussion: *free carbon dioxide, half-bound carbon dioxide* and *bound carbon dioxide*. The free carbon dioxide includes the dissolved carbon dioxide, uncombined and that existing as carbonic acid; whereas by bound carbon dioxide is meant that portion which would remain if the bicarbonate were decomposed to carbonate and free carbon dioxide driven off. By half-bound carbon dioxide is meant that portion which has combined with the bound to yield the bicarbonate. At any one time in the solution no more than two ionic forms of carbon dioxide may exist in appreciable quantities, though the third form is always present in lesser quantities. For example,

in a solution of greater pH than 8.2 (which is the endpoint of phenolphthalein) carbonate and bicarbonate ions predominate, less than pH 8.2 bicarbonate and free carbon dioxide and pH 8.2 mainly bicarbonate.

There is a definite cycle of events involving carbon dioxide and oxygen which takes place within a lake. The bound carbon dioxide is probably little used by aquatic plants but may be used to a certain extent in the building of the shells of animals. Both free and half-bound carbon dioxide are utilized by plants in photosynthesis. During the latter process oxygen is evolved. On the other hand oxygen is removed from the water through the respiration of aquatic plants and animals which in turn give off carbon dioxide. Oxygen is also removed through bacterial action in the decomposition of organic material, again with the formation of carbon dioxide. Thus it may be seen that in a closed system there is a definite relationship between the quantities of these two gases.

During the winter turnover of a lake there is a thorough mixing of the water from top to bottom. The surface water which has been enriched by oxygen from the atmosphere furnishes a supply to the remainder. The carbon dioxide content at the surface is usually small on account of its removal through photosynthetic action in the upper sunlit layer, and its dispersal directly into the atmosphere. During the annual turnover when the water becomes vertically homogeneous, the carbon dioxide content of the rich bottom water becomes diluted, and the surface water correspondingly enriched. Once thermal stratification has become established, though, little gas is added to or removed from the lake, except in the immediate surface layer. Nevertheless changes do occur within the lake and especially during the summer months. The vertical and seasonal variations for Lake Washington have been shown in graphic form. Since it is impractical and unnecessary to include graphs of all the data, only four (February 22, May 30, August 19, and November 18) have been selected to show the seasonal variation (Figs. 3, 4, 5, 6).

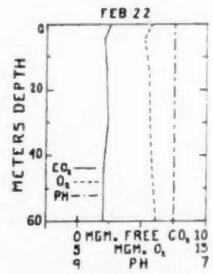

FIG. 3

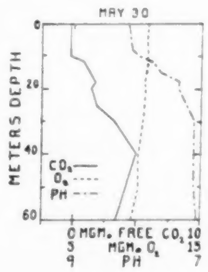

FIG. 4

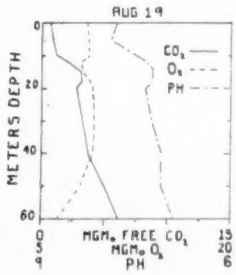

FIG. 5

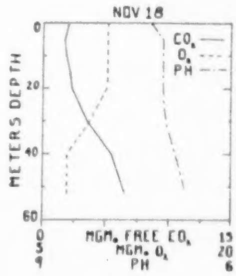

FIG. 6

Dissolved Carbon Dioxide, Dissolved Oxygen and pH at Madison Park. Fig. 3, February 22; Fig. 4, May 30; Fig. 5, August 19; Fig. 6, November 18.

During February, March and April, the surface water was rich in *carbon dioxide* resulting in relatively low pH values of 7 to 7.5. On May 11, for the first time, the supply of free carbon dioxide was depleted in the sur-

face waters because of the active photosynthesis which was taking place. Since the solution now consisted principally of carbonate and bicarbonate ions, the reaction was more alkaline and the pH ranged between 8 and 8.6. The same condition was again noted May 30 and August 1. The remainder of the time there was an excess of free carbon dioxide, though during the summer months it was a very slight excess in the surface waters. This region of diminished carbon dioxide extended through the upper 10 meters of water. As would be expected from a biological consideration there was an increase in the oxygen concentration along with the reduction of carbon dioxide. On the whole there was found a gradual decrease in the oxygen content during the summer. This was probably due in part to the increased temperature (and therefore decreased solubility of atmospheric oxygen) and in part to the oxidation of dead plankton organisms.

In the thermocline from August 1 to September 12 inclusive there was noted an unexpected decrease in oxygen; in this layer oxygen was present in smaller amounts than in the layers immediately above or below. There was also a corresponding increase in the free carbon dioxide. Birge and Juday (1911) noted this same phenomenon in several of the Wisconsin lakes. They have attributed it to the decomposition of particulate organic material whose fall had been retarded or perhaps suspended when coming in contact with the colder and therefore denser water.

During the stratification period of the summer months considerable decomposition takes place in the hypolimnion. Dead plants and animals descend to the hypolimnion and decompose in the bottom waters. This is sometimes called the period of stagnation because of the decomposition and meager circulation in this water layer. This process was observed in Lake Washington.

During the period of homogeneity 2 mg. of free carbon dioxide per liter was a typical value for the bottom waters. Beginning the last of April and lasting throughout the summer this layer showed a considerable increase in free carbon dioxide. At first the rise was most pronounced in the bottom 10 meters of the lake; carbon dioxide-rich water increased to 20 meters in thickness by the middle of August and to 30 meters by October. About this time the epilimnion began to deepen and eventually put the entire body of water into circulation, so that by January 20, the water was again vertically homogeneous. At the peak of decomposition 6 mg. of free carbon dioxide was present near the bottom and 4 mg. throughout the remainder of the hypolimnion.

Again there was a close relationship between the *oxygen* and carbon dioxide. With the great amount of decomposition the supply of oxygen was diminished, though never entirely depleted. The lowest amount recorded at any time near the bottom was 6 mg. and a typical value throughout the

remaining layer was 8 or 9 mg. From these observations it may be concluded that there is ample oxygen to support fish life even at the greatest depths of Lake Washington.

The oxygen has also been calculated on the basis of percentage of saturation. On this basis the water was 85 to 90 per cent saturated during the winter months. Atmospheric oxygen was undoubtedly being taken up by the water but since the temperature was low, the saturation capacity was correspondingly high, and consequently the percentage of saturation did not increase greatly. With the increase in oxygen in April and May due to photosynthesis and with the decreased solubility as a result of warmer water, the percentage of saturation became greater. The water was saturated in the upper 10 meters by April 22, and supersaturated in the upper 5 meters by May 11. Throughout the entire summer until September the upper 10 meters remained practically saturated. Naturally as the supply of oxygen was removed during the summer months in the bottom layer of water by organic decomposition, the percentage of saturation decreased materially. A minimal value of 48% was noted at 60 meters on October 8.

Plant Nutrients

Aquatic plants, like land plants, need nutrient salts for growth. Of these, phosphates, nitrates, and silicates are used in the greatest quantities. Silicates are required by diatoms in the building of their shells. Phosphorus and nitrogen are required for the protoplasm of all plants. The latter elements are supplied by the surrounding water in the form of nitrates and phosphates. As a result of an abundant growth of plankton the supply of these substances in the water may be entirely depleted. Most investigators believe that the growth of plankton ceases when the supply of even one of these necessary or so-called "limiting" nutrients is depleted. However, if one were to consider just the supply of nutrients it would be difficult to explain: first, why the phytoplankton begins to grow more abundantly in the spring whereas an ample supply of food has been available throughout the winter months; second, why there are successive waves of plankton following each other during the growing season; and third, why there is a second pulse of phytoplankton in the fall. The conclusion is necessarily that there must be other limiting factors than the amount of dissolved silicates, phosphates, and nitrates. Perhaps there may be other dissolved substances in amounts so small as to be overlooked, but more likely the limiting factors are physical rather than chemical. Temperature and amount of sunshine are factors that have been suggested. Undoubtedly all must be considered in a study of the growth of plankton, and there are possibly others ignored at present through lack of understanding. In spite of the great amount of work that has already been done along this line of research, a complete explanation is yet lacking.

The total *silicate* content of lake water includes both the ionic and the colloidal forms. Only the ionic form has been evaluated by the method of analysis used for this work; however, it probably is the form of greatest importance to diatom growth. Whenever the available supply of the ionic form is removed, undoubtedly it is replaced to a certain extent by conversion of the colloidal form to the ionic. This may be the reason that water is seldom totally silicate-free. The results of the seasonal study of silicate are shown in Fig. 7.

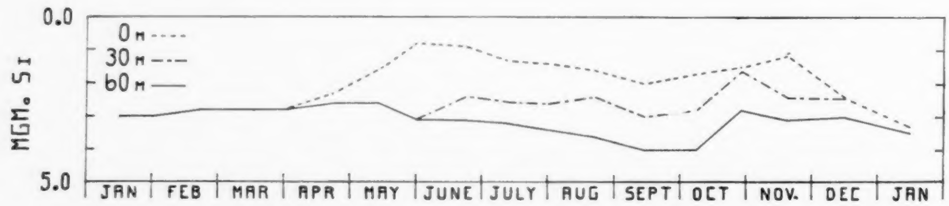

FIG. 7. Seasonal and Vertical Distribution of Silicate at Madison Park.

During the winter the silicate content of the water was about 3 mg. Si per liter. Beginning in April a pulse in diatom growth (Fig. 13) removed considerable quantities of silicate ion. By May 30 the concentration of silicate at the surface, had diminished to 0.8 mg. The diatom growth subsided, and the silicate concentration gradually built up to a maximum of 2.0 mg. in September. Another outburst of diatoms followed, and another corresponding decline in silicate ensued until there was a minimum of 1.2 mg. in the middle of November. The silicate concentration once more increased during the winter turnover of the lake. The bottom waters contained as much as 4.0 mg. Si and never less than 2.8 mg. during this interval. Vertically there was an increase of the silicate concentration with depth though the biggest change occurred in the thermocline. In the epilimnion the change was undoubtedly due to diatom growth, as the maximum abundance of diatoms occurred there. Below the thermocline the gradual increase with depth may be explained by the diffusion of leached silicate from the decaying diatoms, sediment etc. which had fallen to the bottom.

Since the silicate concentration at the surface was never entirely depleted it is hard to believe that it was the limiting factor in the growth of diatoms, unless, of course, a certain threshold value is required for such growth. Rather it is thought that the temperature of the water is of more importance. In the spring the diatom outburst occurred when the temperature rose to 6.5° C. and persisted until a temperature of 12.3° C. was reached. The fall outburst occurred at a temperature of 12.2° C. and persisted to 10.8° C.

Fluctuations in the *phosphate* concentration were quite similar to those just noted for the silicate (Fig. 8). During the winter months 0.008 mg. of soluble PO_4-P was present per liter. Beginning in April the phosphate was reduced in the epilimnion by the abundant plankton growth, and en-

tirely depleted from the middle of June to the middle of November. With the settling and decomposition of dead plankton the hypolimnion began to acquire increased quantities of phosphate, particularly near the bottom. By the middle of July a maximum value of 0.025 mg. per liter was noted here. At first the high phosphate layer on the bottom was quite thin, but it gradually increased, until by the middle of September it reached halfway to the surface, that is to the 30 m. level.

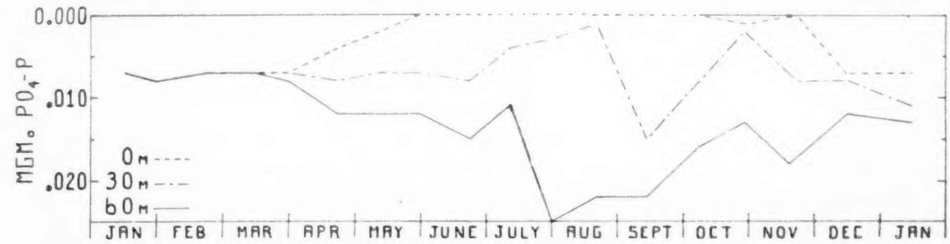

FIG. 8. Seasonal and Vertical Distribution of Phosphate at Madison Park.

Since the phosphate was reduced to zero concentration it could possibly be considered a limiting factor. However, there was a persistent growth of plankton, though to be sure a small one, during this period of low phosphate values. It should be mentioned that just because phosphate was not detected by our method of analysis it was no proof that plankton was not utilizing phosphate during growth. It is quite possible that a small amount of phosphate was being released from decomposing plankton in the epilimnion but did not have an opportunity to accumulate, as it was being extracted immediately by the growing plankton.

A seasonal study has also been made of the *nitrates* (Fig. 9). There is a greater amount of nitrate present than phosphate though not nearly as much as silicate. Until the middle of April about 0.10 mg. NO_3-N was present per liter of water. At that time the surface supply began to diminish and by the middle of July none remained. From that time until December very little was present, amounting usually to about 0.04 mg. Whereas the bottom waters were enriched during the summer months with silicate and phosphate, the quantity of nitrate in the bottom water remained fairly constant at 0.12 mg. until the first of July, then decreased to 0.06 or 0.04 mg. and maintained that figure throughout the remainder of the year. This is not a large decrease, but seems to be a significant one.

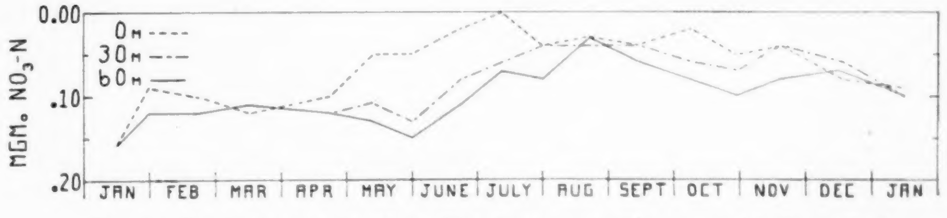

FIG. 9. Seasonal and Vertical Distribution of Nitrate at Madison Park.

Ammonia and *nitrite* are sometimes products of denitrification. These substances were determined in Lake Washington. Neither was ever present in an appreciable quantity. Occasionally as much as 0.02 mg. of NH_3-N was present though usually there was less than 0.01 mg. and most of the time none could be detected. Because such small amounts were present, no conclusions can be made with regard to seasonal variation. No nitrite could be detected throughout the year except in three samples: at 15 to 18 meters on May 11, May 30, and June 21; and then only 0.001 mg. NO_2-N was found.

Organic Material

Extensive studies have been made in the past of the *organic material* of lakes for it comprises the food supply of certain aquatic animals. Organic material includes soluble and colloidal organic compounds and particulate matter. The latter is made up of plankton both living and dead, and debris. No attempt has been made in this investigation to distinguish between these various forms. That is, the plankton and filterable suspended material have not been separated from the dissolved material in the samples before chemical analysis.

One of the means of measuring the amount of organic material is to determine the "oxygen consumed." This is the amount of oxygen supplied by acid permanganate in a specified time at 100° C. in oxidizing the organic material. It should be noted that inorganic as well as organic reducing substances in the water sample are also oxidized and so would frustrate the purpose of the determination but, except under unusual conditions, such substances are not normally present. Although no information is gained from this determination concerning the specific compounds causing the reducing action, an indication is given regarding the quantity of dissolved organic material.

Oxygen consumed was determined for thirteen series of samples. No great seasonal variation was apparent. (Fig. 10.) The variation was only between 1.2 and 2.3 mg. of oxygen per liter, both of which are rather small values. There was usually a small increase in the oxygen consumed with increase in depth. It has already been shown that during the summer months near the bottom there was a decrease in the dissolved oxygen due to the decomposition of organic material. However, this was not accompanied by any change in the oxygen consumed.

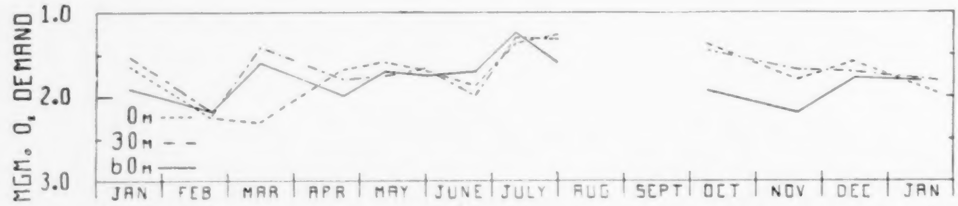

FIG. 10. Seasonal and Vertical Distribution of Oxygen Consumed at Madison Park.

Juday and Birge (1932) have made oxygen consumed determinations for the Wisconsin lakes. They found that values for the various lakes ranged between 1.2 and 34.5 mg. of oxygen per liter. An average was not stated, but it would not be far from 6 or 7 mg. Conclusions from their studies were: first, that the oxygen demand could be correlated with the color of most lakes and, second, that on an average 1 mg. of organic carbon per liter was present for each mg. of oxygen consumed. Individually there were wide deviations from the latter conclusion. On the basis of this conclusion the organic carbon content for Lake Washington would be from 1 to 2 mg. per liter. This has not been verified by more direct means.

The utilization of phosphates and nitrates in the growth of plankton has been amply demonstrated. It is also known that nitrates and phosphates are later released or regenerated from their organic combinations. To get a complete picture of the potential food supply of the plankton it is necessary not only to know the amount of the phosphate present but also the organic phosphorus content of the lake; and not only the nitrate, but also the other forms of nitrogen present which include the organic nitrogen. For some time the importance of organic nitrogen in the aquatic nitrogen cycle has been appreciated but it is only recently that organic phosphorus has been receiving similar attention.

Birge, Juday, *et al.* (1928) found that the Wisconsin lakes possess larger quantities of phosphorus in the organic form than in the inorganic. *Organic phosphorus* has been determined on Lake Washington waters throughout the year to note seasonal variation. (Fig. 11.) The quantity varied between 0.000 and 0.022 mg. per liter. Similar values have been found in many of the Wisconsin lakes. There was no noticeable vertical distribution. When an average was taken for the individual depths, it was found to be 0.012 mg. for each. There was no apparent seasonal variation. The fact that the organic phosphorus did not increase proportionally with the growth of plankton indicates that the plankton must fall quickly to the bottom. This same conclusion also follows from the rise in the soluble phosphate in the bottom waters shortly after the growth of plankton in the surface waters.

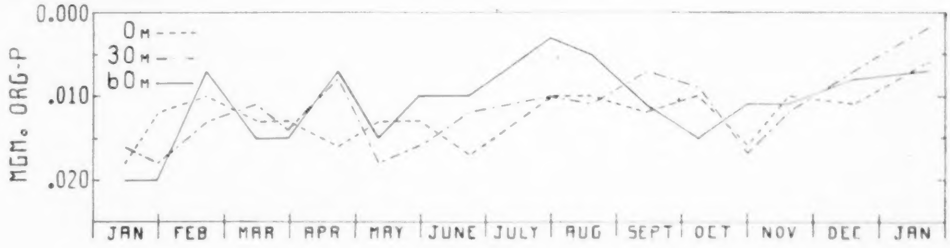

Fig. 11. Seasonal and Vertical Distribution of Organic Phosphorus at Madison Park.

As in the case of the organic phosphorus the results for organic nitrogen varied widely. The extremes were 0.07 and 0.23 mg. N per liter. No corre-

lation could be made with depth nor with season. (Fig. 12.) The average throughout the year for each depth was found to be 0.14 mg. N, which was also the average for the lake as a whole. This value is approximately the same as the lowest organic nitrogen values found for the northeastern Wisconsin lakes.

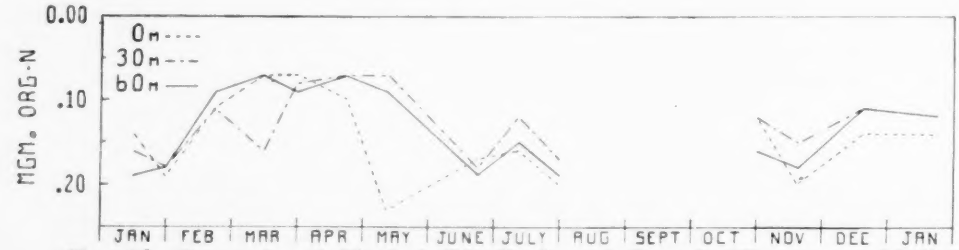

FIG. 12. Seasonal and Vertical Distribution of Organic Nitrogen at Madison Park.

Redfield (1934) calculated the N/P ratio from the nitrate and phosphate content of the Atlantic Ocean waters. He also calculated the N/P ratio from the organic N and organic P of marine plankton. In each case it was 15/1. This is an interesting observation as it demonstrates the influence of environment upon the composition of plankton. The ratio of organic N to organic P in Lake Washington water was 12 to 1, a value quite similar to that in the plankton of the Atlantic Ocean. During the months when there was little plankton activity and no stratification in Lake Washington, the ratio was exactly 15 to 1. The conclusion is that although the concentrations of nitrate and phosphate are much smaller in Lake Washington than in ocean water, the ratio of N to P is essentially the same in both.

THE PLANKTON

THE QUANTITY OF PLANKTON

The quantity of plankton in Lake Washington as determined by weighing is shown in Table 5 and Fig. 13. The values for Madison Park, North Point, and South Point were quite similar except that the spring maximum was two weeks earlier at North Point than at Madison Park. The amount of plankton in the deep 60-30 meter stratum of water at Madison Park was less than one-quarter of that in the upper stratum (30-0 meters). It may be of interest here to compare the values obtained by Birge and Juday (1922) on Lake Mendota with those found on Lake Washington in the 30-0 m. stratum at Madison Park. Yearly average in mg./ cu.m.:

	Dry net plankton	*Organic matter*	*Ash*	*% Ash*
Mendota	491	310	181	37
Washington	150	58	92	61

It may be seen that the net plankton of Lake Mendota is 3 to 5 times richer, depending upon the basis of comparison, than that of Lake Washington. We have previously pointed out that the values for "oxygen consumed" in

Lake Washington are about one-third those of the Wisconsin lakes. The higher percentage of ash in the Lake Washington plankton can be attributed to the dominant role played by the diatom flora throughout the period of plankton growth. Only during the four summer months was the ash less the organic matter composed 85% of the total plankton, Fig. 14. The amount than half of the total plankton. In late summer, when diatoms were scarce, of plankton in Lake Washington could doubtless be more favorably compared with that in a deeper body of water than Lake Mendota, say Lake Michigan, but no figures are at hand for this purpose. In connection with this subject two lakes in the Puget Sound area may be mentioned which illustrate the extremes of poor and rich plankton production—Crescent Lake, with a depth of 190 meters, distinctly oligotrophic; and Echo Lake, with a depth of 10 meters, distinctly eutrophic (Scheffer 1933, 1935).

TABLE 5. WEIGHT IN MILLIGRAMS OF PLANKTON OBTAINED BY HAULING A NET VERTICALLY THROUGH 30 METERS AND THUS FILTERING APPROXIMATELY 750 LITERS OF WATER; JANUARY, 1933 TO JANUARY, 1934.

Date	Madison Park lower stratum 60-30 m.			Madison Park upper stratum 30-0 m.			North Point 30-0 m.			South Point 30-0 m.		
	Dry Plankton	Ash	Organic Matter	Dry Plankton	Ash	Organic Matter	Dry Plankton	Ash	Organic Matter	Dry Plankton	Ash	Organic Matter
January 14......	22	10	12	123	86	37	82	54	28	62	38	24
January 28......	30	17	3	100	71	29	102	67	35	91	59	32
February 22......	37	21	16	152	110	42	85	53	32	114	80	34
March 14......	23	13	10	90	57	33	135	86	49	131	82	49
April 1......	45	29	17	73	53	20	117	55	62	118	49	69
April 22......	28	19	9	161	93	69	133	92	40	....	....	....
May 11......	62	44	18	248	171	77	473	309	164	267	187	80
May 30......	81	57	24	483	310	173	358	188	170	....	....	....
June 21......	39	22	18	61	19	42	45	20	25	58	17	41
July 12......	17	10	7	41	8	33	39	8	31	....	....	....
August 1......	9	3	6	24	7	18	26	4	21	39	6	33
August 19......	7	3	4	46	3	43	21	4	17	....	....	....
September 12......	3	2	1	21	2	19	29	3	26	....	....	....
October 8......	7	6	1	31	14	17	36	23	13	75	25	50
October 28......	19	15	4	227	155	72	274	164	110	162	119	43
November 18......	16	9	7	118	76	42	138	85	53	....	....	....
December 16......	10	2	8	22	4	18	38	11	27	22	6	16
January 20......	6	3	3	10	2	8	14	3	11	11	2	9

Summary of the above figures, with weights expressed as mg. per cu. m.:

Total............	615	379	236	2,704	1,650	1,215	2,850	1,635	1,215	(South Point data not comparable)
Average...........	34	21	13	150	92	58	159	97	62	
Maximum.........	107	75	31	642	412	230	629	410	226	
Minimum.........	4	3	1	13	3	11	19	4	15	

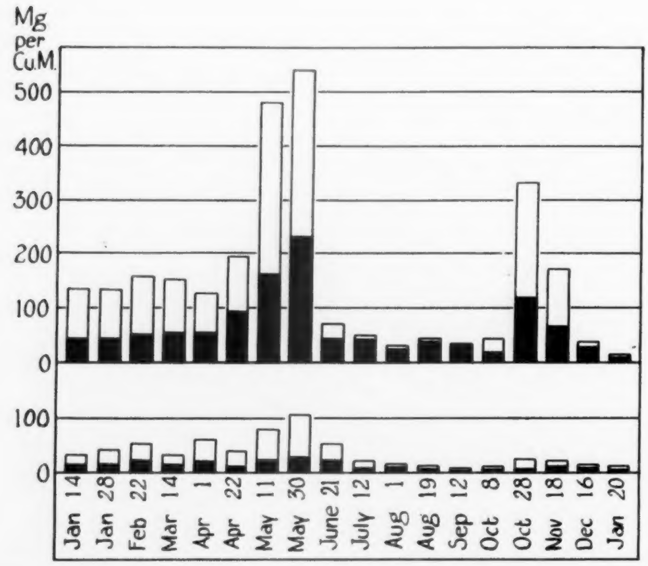

FIG. 13. The quantity of plankton in Lake Washington from January, 1933, to January, 1934. The upper diagram shows the average weight of plankton in the upper 30 meters of water at Madison Park and North Point. The lower diagram shows the weight in the bottom 30 meters (60 to 30) at Madison Park. The organic component is represented by black, the ash by white.

The seasonal variation of the plankton in Lake Washington is represented in Fig. 13. A spring maximum occurred in May, a summer decline from June to September, and a fall maximum in October and November. The amount of plankton at the close of the season did not rise to its value of a year previous, for an undetermined reason. It was observed, however, that in the process of counting plankton organisms from this sample diatoms were much scarcer than in the previous January, as were also copepods. An excess of 9.7 inches of rain above normal in the month of December, 1933, may have had some effect in limiting the growth of plankton at this particular time.

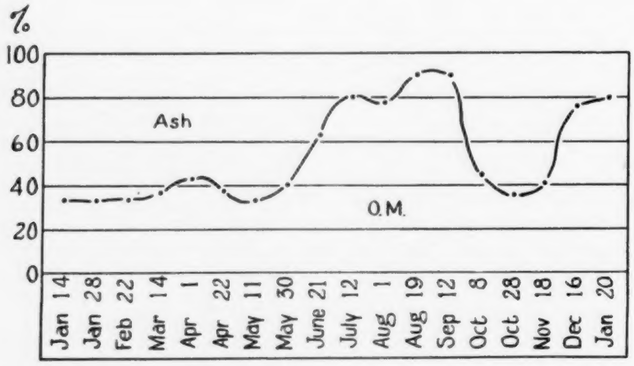

FIG. 14. The relative proportion of organic matter to ash in the total plankton from the upper 30 meters of water at Madison Park and North Point. The area above the line represents ash, below, organic matter.

THE PLANKTON AS A POPULATION

Only the true plankton organisms are discussed in this paper, that is, those which were taken in net hauls from the open waters of the lake. Altogether 107 species were distinguished in the plankton (Fig. 15). The algae included 72, the protozoa 6, the rotifera 17, and the crustacea 12,—or phytoplankton 72, zooplankton 35. Eddy (1927) found in the net plankton of Lake Michigan a total of 119 species.

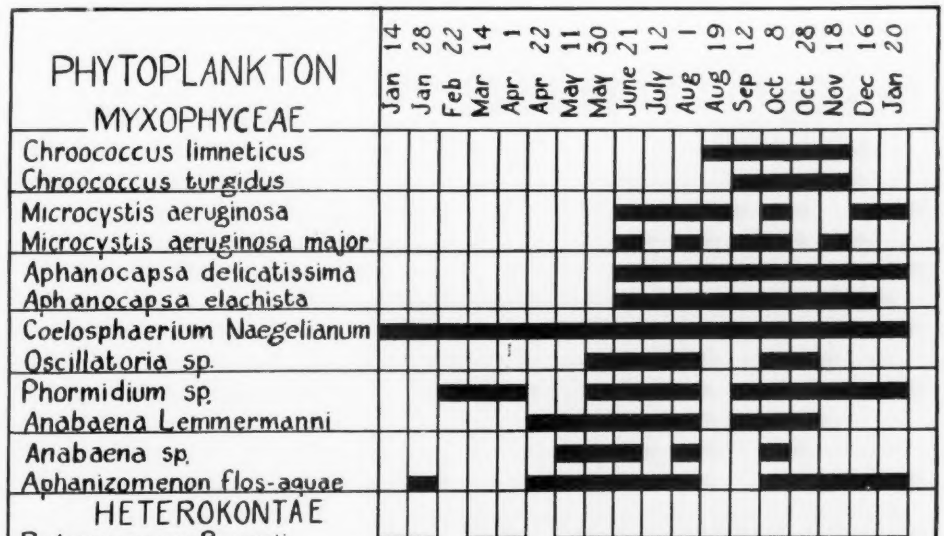

FIG. 15. Composition of the plankton from January, 1933, to January, 1934.

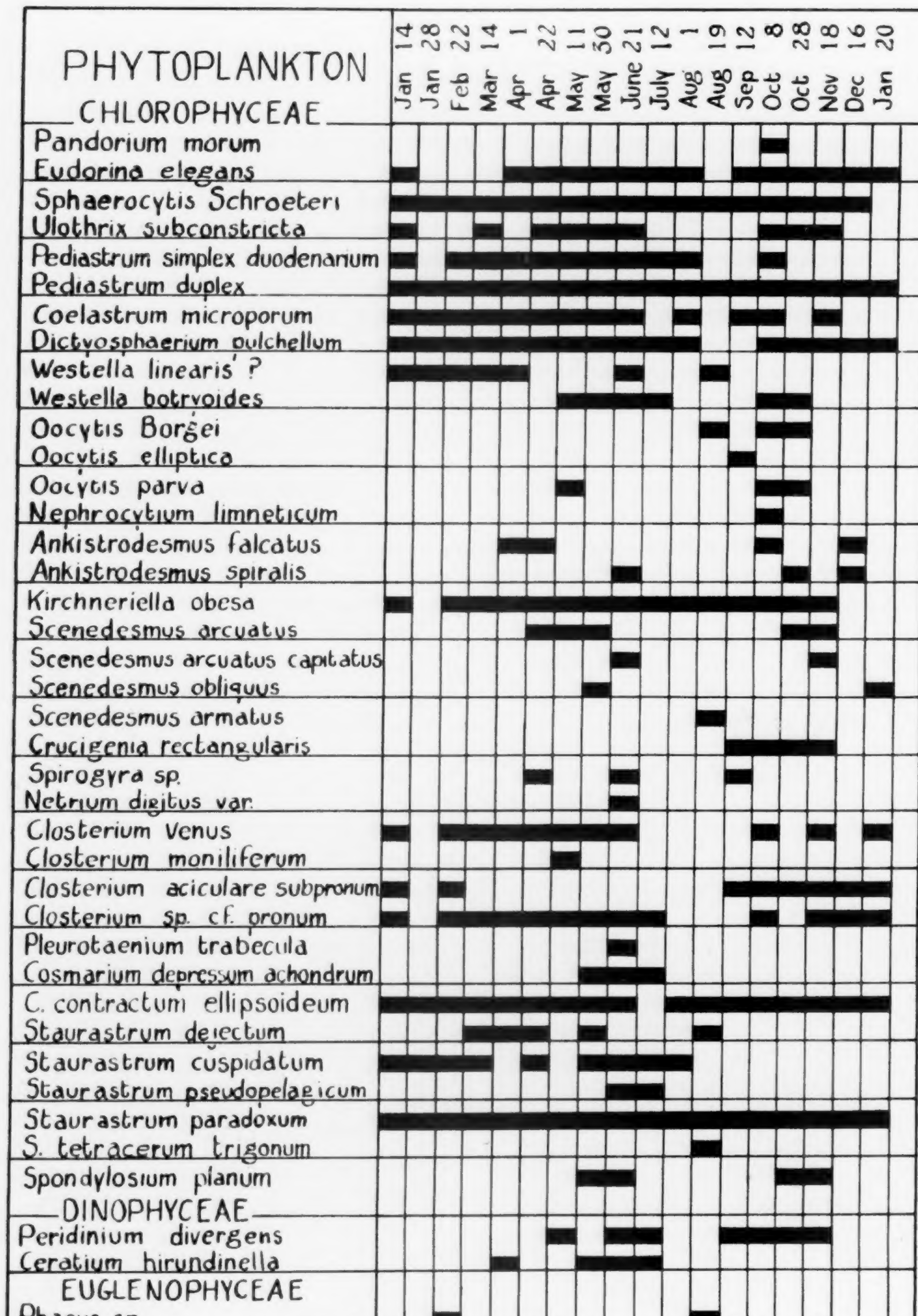

FIGURE 15 (Continued)

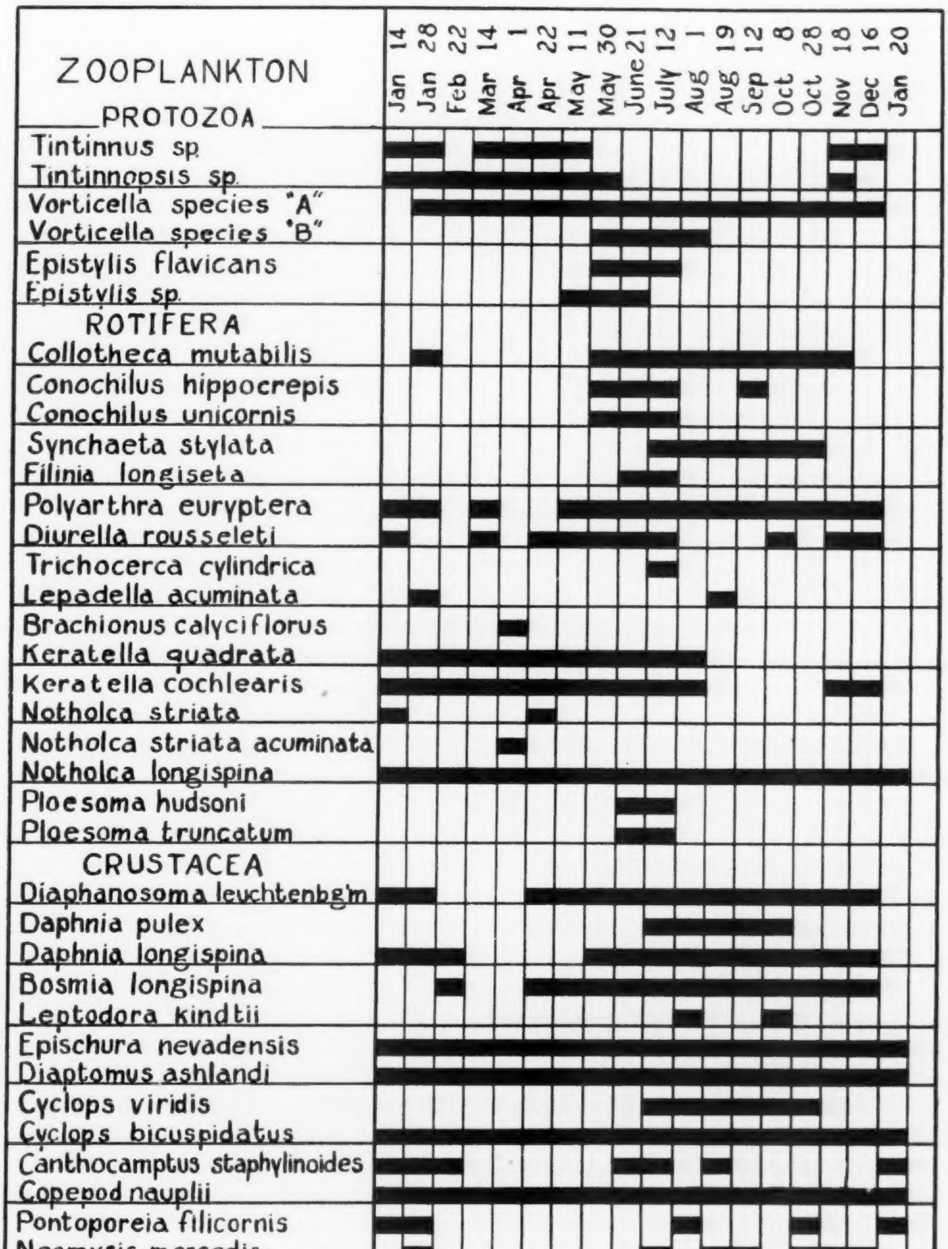

FIGURE 15 (Continued)

The total number of species found in the plankton population of Lake Washington showed a variation with the season. During the winter the plankton was composed of from 40-50 species, in June up to 74 species, in late summer 40-50 species again, and in October up to 62 species.

The plankton was quite uniformly distributed over the lake. North Point and South Point are 18 miles apart, yet the plankton was almost identical

at both sites. The appearance of certain warm-water rotifers and protozoa, however, was noted two weeks earlier at the shallower end stations than at Madison Park.

The question of stability or continuity of the plankton population over a period of years was of much interest. Scattered observations made on nearby Echo Lake, a smaller body of water, indicate that the character of the plankton changes noticeably from year to year. In other words the plankton complex during the spring season of the year may present a different picture in the spring season of the next year, although of course many of the same species may appear in both cases. Fortunately the work of Kemmerer (1923) on Lake Washington 20 years ago has furnished a picture of the plankton at that time which may be compared with the results of the present study. He found in the net plankton of August 9, 1913, the following organisms:

Plants	*Animals*
Asterionella	Anuraea (Keratella)
Cyclotella	Notholca
Pediastrum	Epischura
Staurastrum	Cyclops
Aphanizomenon	Copepod nauplii
Anabaena	Diaphanosoma
Ceratium	Bosmina

The same genera were present in the plankton in August, twenty years later, with the exception of Ceratium, which, however, had been present in July. In addition Diaptomus and Daphnia were present in 1933 in small numbers, though not mentioned by Kemmerer. Eddy (1927) in a study of the plankton of Lake Michigan states that "Comparisons of recent collections with those made forty years ago show that very little change has occurred in the general composition of the plankton."

With regard to the population and general behavior of its plankton Lake Washington falls into a class with the Great Lakes. Strong similarities appear between the phytoplankton of Lake Washington and that of Lake Superior (Taylor 1935) or Lake Erie (Tiffany 1934). In addition the work of Eddy (1927) on both the phyto- and zooplankton of Lake Michigan shows that not only the great majority of genera are common to both lakes, but many species as well. By way of illustration, the genera of plankton organisms common to both Lake Washington and Lake Michigan are listed as follows:

MYXOPHYCEAE

Coelosphaerium	Anabaena
Aphanocapsa	Oscillatoria
Chroococcus	

Baccilarieae

Melosira	
Cyclotella	Fragilaria
Stephanodiscus	Synedra
Tabellaria	Asterionella

Chlorophyceae
(and related groups)

Closterium	Coelastrum
Spirogyra	Scenedesmus
Cosmarium	Crucigenia
Dictyosphaerium	Pediastrum
Botryococcus	Eudorina
Kirchneriella	Phacus
Oocystis	Dinobryon
Sphaerocystis	Ceratium
Ankistrodesmus	Peridinium

Protozoa

Vorticella

Rotifera

Synchaeta	Keratella
Polyarthra	Notholca
Diurella	Brachionus
Trichocerca	Filinia
Lepadella	Conochilus

Cladocera

Diaphanosoma	Bosmina
Daphnia	Leptodora

Copepoda

Epischura	Cyclops
Diaptomus	Canthocamptus

The composition of the plankton with respect to the species present at various seasons is summarized in Figs. 16, 17, and 18. Generally speaking, the classes of plankton organisms behave throughout the year as follows:

1. Blue-green algae: common in summer and fall, the warmer months.
2. Diatoms: common throughout the year except in midsummer; a great pulse in early spring and a lesser one in fall.
3. Green algae: in late spring, especially, and in fall.
4. Protozoa: only a few species, but appearing sporadically in large numbers in summer.
5. Rotifera: several year-round species only slightly affected by changing water conditions; many other species appearing for brief periods in summer.
6. Cladocera: in summer and fall; seldom in the deeper waters.
7. Copepoda: Cyclops fairly uniform but seeking lower levels in summer. Diaptomus fluctuating with the diatom pulses, and giving way to Epischura during the summer.
8. Neomysis: in all months of the year, at depths greater than 30 meters.

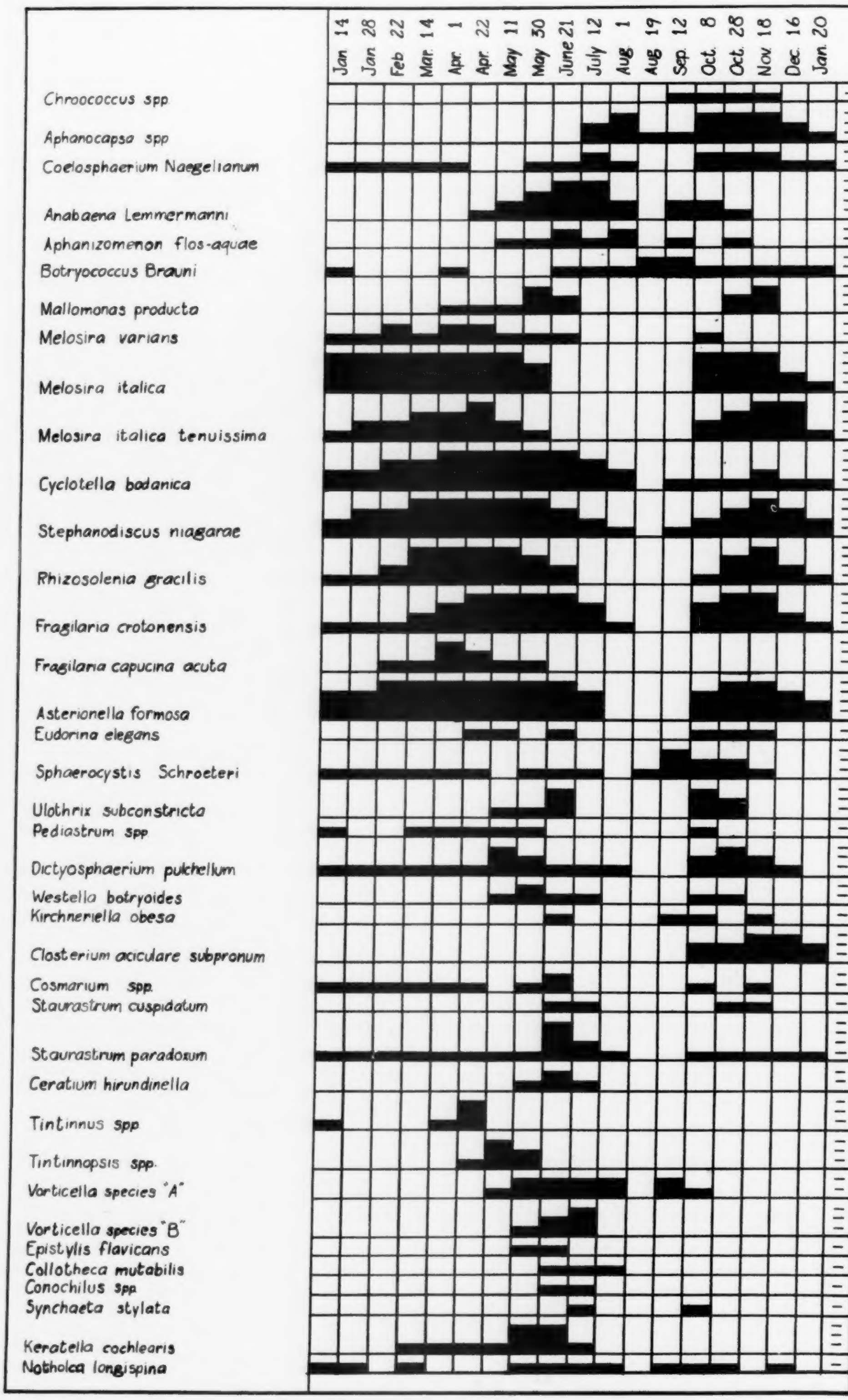

FIG. 16. Seasonal occurrence of the more abundant plankton species (excluding the crustacea). The black bars of four different thicknesses denote occurrence as occasional, common, very common, and abundant.

THE SPECIES OF PLANKTON ORGANISMS

For each species there is given below (1) the dimensions of the organism (in 4% formalin), (2) the seasonal occurrence in Lake Washington, and (3) a reference to the species in previous literature. These data are given for the following purposes: (1) to record the size of each Lake Washington species so that anyone so desiring may compare it with the size of the species as recorded from other parts of the country, (2) to indicate the season of the year when apparently a species finds in the water the

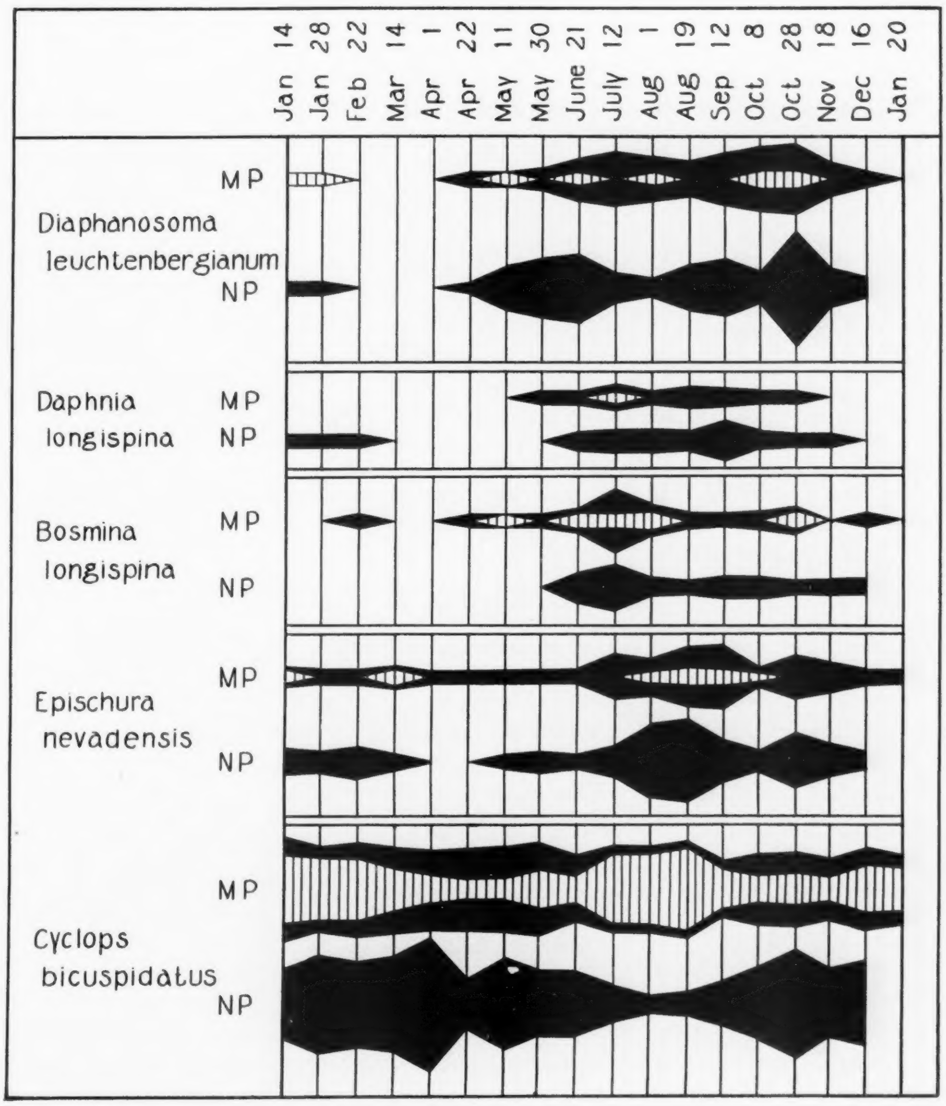

FIG. 17. Seasonal occurrence of the more abundant species of crustacea in the plankton at Madison Park and North Point. The North Point hauls are from a vertical column of water 30 meters to the surface. The Madison Park hauls combine a lower (60 to 30 m.) and an upper (30 to 0 m.) haul. The curves for the deeper hauls are shown by barred lines.

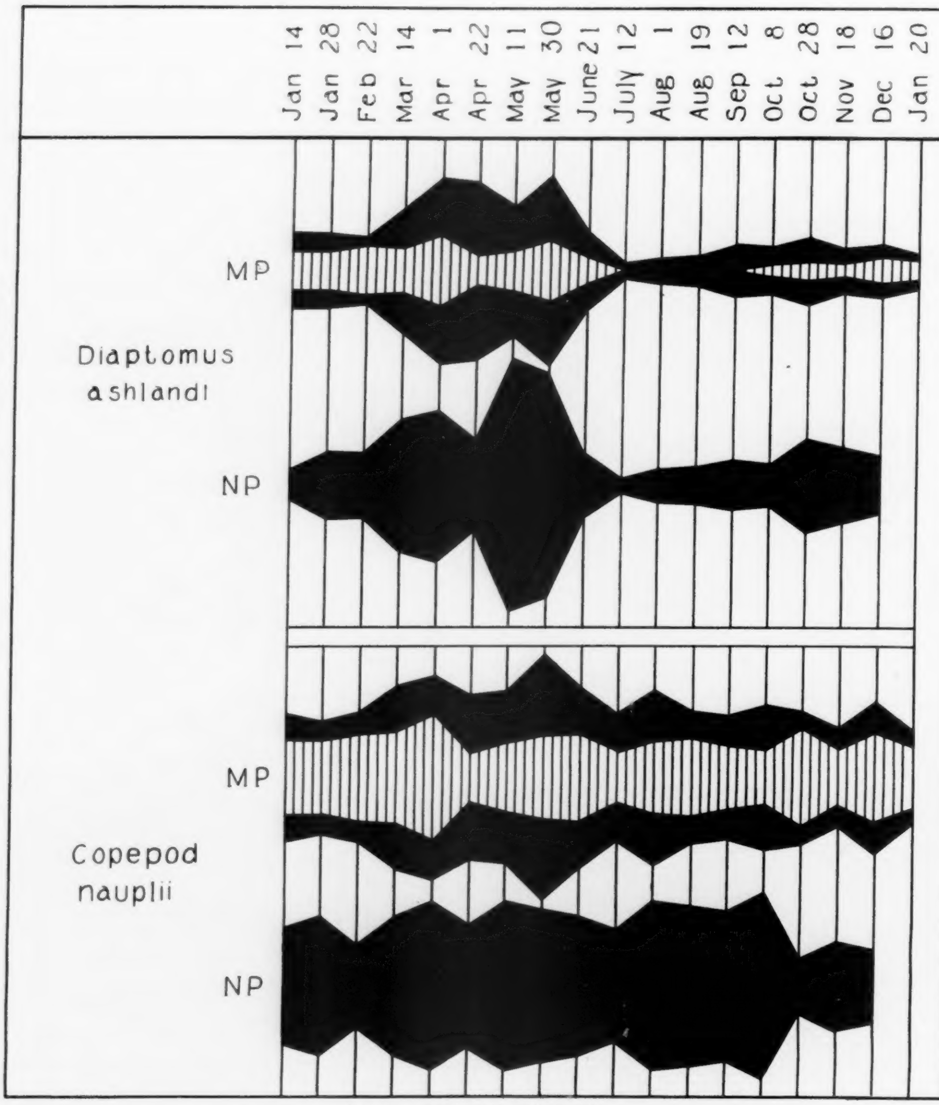

FIGURE 17 (Continued)

most favorable conditions for its growth, (3) to give the source in previous literature of a more complete description of each organism than is practicable in the present paper.

MYXOPHYCEAE

Chroococcus:

C. limneticus Lemmermann. Diam. cells without sheath 9.5-10.5 mu; sheath 0.5-3 mu. Usually in colonies of 4 pairs. Occasional, in fall. Smith 1920.

C. turgidus (Kütz.) Nägeli. Diam. cells without sheath 10-17 mu; sheath 1.5 mu. Usually in colonies of 4-8 pairs. A specimen of intermediate size and with lamellae poorly defined cannot be with certainty distinguished from the preceding species. Occasional, in fall. Smith 1920.

Microcystis:

M. aeruginosa Kützing. Diam. colony 75-180 mu; cells 2.3-3 mu, and up to 3.5 mu long when subspherical. Rare, in fall. Smith 1920.

M. aeruginosa var. *major* (Wittrock) G. M. Smith. Diam. colony 30-100 mu; cells 4.8-6 mu. Rare, in fall. Smith 1920.

Aphanocapsa:

A. delicatissima W. & G. S. West. Diam. colony 15-50 mu; cells 0.7-0.75 mu, and up to 1.5 mu long before dividing. Very common in fall. Smith 1920.

A. elachista W. & G. S. West. Diam. colony 75-350 mu; cells 1.6-2.2 mu. Very common in fall. Smith 1920.

Coelosphaerium:

C. Naegelianum Unger. Diam. colony 55-275 mu; cells 3.5-7 mu. Common throughout the year, especially in July and in the fall. Smith 1920.

Oscillatoria:

An undetermined species. Length of trichomes 600-800 mu; diam. 7.5-10.5 mu. Rare, in summer and fall. Smith 1920.

Phormidium:

An undetermined species. Trichomes long and thready; diam. without sheath 1.3-1.6 mu, with sheath 1.8-2.6 mu; of cells 1.1-3.6 mu; space between trichomes 30-40 mu. Rare, throughout the year. Smith 1920.

Anabaena:

A. Lemmermanni P. Richter. Trichomes long and coiled; diam. cells 6 mu; heterocysts 7 mu; spores 9-10 x 19-32 mu. Up to 75 spores in one cluster. Abundant in early summer and very common again in fall. Spores first noted in June and July, and last in October. Smith 1920.

An undetermined species. Trichomes short and straight, often parallel; cells 8.5-10.4 mu; heterocysts 11.6 mu. No spores observed. This is possibly *A. planctonica* Brunnthaler. Rare, in summer. Smith 1920.

Aphanizomenon:

A. flos-aquae (L) Ralfs. Diam. cells 5 mu; heterocysts 6.5 x 16 mu. Occasional to common, in summer. Smith 1920.

HETEROKONTAE

Botryococcus:

B. Braunii Kützing. Diam. simple colonies 100-170 mu; compound colonies microscopic; cells 4.5 x 10 mu. (Several colonies were noted with larger cells 6.5-8 x 14 mu, which might better be referred to *B. protuberans*.) Occasional throughout the year; common in midsummer. Smith 1920.

CHRYSOPHYCEAE

Mallomonas:

M. producta (Zacharias) Iwanoff. Cells 11 mu broad; 32-54 mu long; as many as 40 spines, up to 40 mu long. Occasional to very common in spring and fall. Smith 1920.

Dinobryon:

D. sertularia Ehrenberg. Receptacles 9 x 38 mu. Noted only twice, in May. Smith 1920.

Chrysamoeba:

An unidentified species. Cells 12-16 x 13-21 mu, yellow-green to brown, in a transparent gelatinous sheet 60-100 mu in diameter. Single or in clusters of as many as 8. Gelatinous strands often covered with debris. Occasional throughout the year, common in May. Smith 1920.

Rhizochrysis:

R. limnetica G. M. Smith. Cells 19 mu; spines (pseudopodia?) 20-35 mu long, stiff but moving freely from base. Pale yellow-green, one large and several smaller green chloroplasts. Several observed, on June 21. Smaller than described by Smith 1920.

BACCILARIEAE

For identification of the diatoms we are indebted to H. E. Sovereign who has made extensive studies of the diatoms of lakes, bogs, and peat deposits along the Pacific Coast. We are also indebted to Dr. G. Dallas Hanna for advice on technique.

In addition to the true open-water species there were observed in the plankton from time to time 35 forms of littoral diatoms representing 15 rather cosmopolitan genera. Discussion of these is omitted as being outside the scope of the present paper. The shallow water or benthic genera included:

Cocconeis	Gomphoneis
Cymatopleura	Navicula
Cymbella	Nitzschia
Diatoma	Pinnularia
Diploneis	Rhoicosphenia
Epithemia	Stauroneis
Eunotia	Synedra
Frustulia	Surirella

Three of the common limnetic diatoms, *Stephanodiscus astraea* and variety *minutula*, and *Cyclotella ocellata* were too minute to be counted in water mounts and thus their seasonal distribution is not revealed. However, an examination of hyrax-prepared slides showed the presence of all

three in every month of the year. Altogether they constituted an estimated 5% or less of the total numbers of *Stephanodiscus niagarae* present, taking this common species as a relative index.

Melosira:

M. varians C. A. Agardh. Fig. 18. Diam. 13-37.8 mu; length 24 mu. Occasional to common, except in summer. Hustedt 1930.

M. italica (Ehr.) Kütz. Figs. 19, 20. Diam. 5-16.5 mu; length 8-18 mu; perivalvar rows 18 in 10 mu; cross rows 17 in 10 mu; about 15 spines on end. Dominant in winter, giving way to Asterionella in May; absent in summer; abundant in fall. Auxospores appeared in April-May and in October. Hustedt 1930.

M. italica var. *tenuissima* (Grun.) O. Müller. Fig. 21. Diam. 4-5 mu; length 20-30 mu; perivalvar rows 15 in 10 mu; cross rows 15 in 10 mu. Occurs with the species and grades into it. Hustedt 1930.

Cyclotella:

C. ocellata Pant. Figs. 22, 23. Diam. 11-21 mu; circumferential striae 16 in 10 mu. Rare to occasional in all months of the year. Hustedt 1930.

C. bodanica Eulenst. Figs. 24, 25. Diam. 24-48 mu; radial striae 10 in 10 mu. Differs from Hustedt's description only in having wider striae. Very common in spring, becoming abundant in May; occasional in fall. Hustedt 1930.

Stephanodiscus:

S. niagarae Ehr. Figs. 26, 27. Diam. 58-97 mu; radial punctae 15 in 10 mu; spines 1.4 in 10 mu. Larger than described in Elmore. Occasional to common throughout the year, becoming abundant in May and November. Elmore 1921.

S. astraea (Ehr.) Grun. Figs. 28, 29. Diam. 36-53 mu; radial punctae 15 in 10 mu. Rare to occasional throughout the year. Hustedt 1930.

S. astraea var. *minutula* (Kütz.) Grun. Figs. 30, 31, 32. Diam. 15-30 mu; radial punctae 15 in 10 mu. Distinguished from the species only by size. Rare to occasional throughout the year. Hustedt 1930.

Rhizosolenia:

R. gracilis H. L. Smith. Fig. 33. Diam. 4-12 mu; length 100-230 mu. Common to abundant in spring and fall; absent in summer. Hustedt 1930.

Fragilaria:

F. crotonensis Kitton. Fig. 34. Length 45-73 mu; width in middle 2.6 mu, at ends 1.5 mu; striae 17 in 10 mu. Throughout the year; dominant in April-May, and in October-November. Hustedt 1930.

F. capucina Desmazières var. *acuta* Grun. Fig. 35. Length 18-80 mu; width, 2.6 mu; striae 15-19 in 10 mu. In spring only, becoming very common in early April a month before *crotonensis*. Hustedt 1930.

Tabellaria:

T. fenestrata (Lyngb.) Kütz. Fig. 36. Length 35 mu; width 11 mu. Rare, in warmer months. Hustedt 1930.

Asterionella:

A. formosa Hassall. Fig. 37. Length 45-84 mu; width at ends 3.7 and 5.2 mu, at middle 3.1 mu. Striae 26 in 10 mu. Common to abundant in all months but August and September; dominant in April, following Melosira and preceding Fragilaria. Hustedt 1930.

Synedra:

S. ulna (Nitzsch) Ehr. var. *danica* (Kütz.) Grun. Fig. 38. Length 200-408 mu; width 4.8-6.7 mu; striae 11-12 in 10 mu. Scattered occasionally throughout spring and fall. Hustedt 1930.

Unidentified species were noted in small numbers throughout the year. One was a common epiphyte on Melosira. Another formed rosettes (Fig. 39) of up to 50 cells. Length 25-32 mu, width 2.5 mu. Occasional in April and in September-October.

CHLOROPHYCEAE

Pandorina:

P. morum Bory. Diam. individual colonies 30-36 mu; cells 7.5-8 mu. One seen, in October. Smith 1920.

Eudorina:

E. elegans Ehrenberg. Diam. colony 60-100 mu; cells 12-16 mu. Scattered rarely throughout the year, occasional in April-June and October-November. Smith 1920.

Sphaerocystis:

S. Schroeteri Chodat. Diam. colony 50-120 mu; cells 13-18 mu; daughter cells as small as 6 mu, in a morula-like cluster. The envelope may be loose or firm; spherical or elongated. Occasional throughout the year, becoming very common in September. Smith 1920.

Ulothrix:

U. subconstricta G. S. West. Filament long and thready; diam. cells 4.5-7 mu; length 8-24 mu. Rare throughout the year, becoming very common for brief periods in June and October. Smith 1920.

Pediastrum:

P. simplex var. *duodenarium* (Bailey) Rabenhorst. Cells 9-15 mu broad; faintly punctate. Occasional in nearly all months of the year. Smith 1920.

P. duplex Meyen. Cells 11-20 mu broad; punctate; varying greatly in shape. Slightly more common than *P. simplex*, occasional in every month of the year, especially in spring. Smith 1920.

Coelastrum:

C. microporum Nägeli. Diam. colony 45-60 mu; cells 13-16 mu; daughter cells 3.5 mu. Rare, in nearly all months of the year. Smith 1920.

Dictyosphaerium:

D. pulchellum Wood. Diam. colony ca. 55 mu; cells 5-7.2 mu, or when immature and subspherical 4.6-4.8 x 4.8-7.2 mu. Occasional except in midsummer; very common in May and October. Smith 1920.

Westella:

W. linearis G. M. Smith. Cells subspherical, 3.7 x 4.3 mu; yellow-green; one chloroplast; no visible pyrenoids; cell wall thick and distinct, surrounded by a delicate, continuous gelatinous sheath. In strands of 2-20, often parallel. This species agrees with the dimensions given by Smith (1920) but not by the same author (1933). Cells are in more or less straight lines but not usually in groups of 4. Rare, in winter and spring.

W. botryoides (W. West) de Wildeman. Diam. cells 6.5-9 mu. Similar in appearance to Sphaerocystis but with cells usually in groups of 2-4 and scattered loosely in an irregular colony. There is no colonial envelope, but faint gelatinous strands (the old mother cell walls) holding the cells together. Occasional in early summer and October. Smith 1920.

Oocystis:

O. Borgei Snow. Diam. colony 35-120 mu; cells 12-16 x 18-19 mu; 3 or 4 chloroplasts. Rare, in August and October. Smith 1920.

O. elliptica W. West. Diam. colony 45-52 mu; cells 16-18 x 22-24 mu; from 15 to 40 chloroplasts. Rare, in September. Smith 1920.

O. parva W. & G. S. West. Diam. colony 18-40 mu; cells 6-8.5 x 9-12 mu; one chloroplast. Rare, in May and October. Smith 1920.

Nephrocytium:

N. limneticum G. M. Smith. Compound colony 65 x 75 mu; cells 4 x 10 mu. One seen, October. Smith 1920 (as Gleocystopsis); Smith 1933.

Ankistrodesmus:

A. falcatus (Corda) Ralfs. Cells 1.5-3.5 x 50-70 mu. Scattered rarely throughout the year. Smith 1920.

A. spiralis (Turner) Lemmermann. Cells 2 x 45 mu. Scattered rarely throughout the year. Smith 1920.

Kirchneriella:

K. obesa (W. West) Schmidle. Diam. cells 7-12 mu, breadth 3-6 mu; 15-30 in loose colony. Rare throughout the year, becoming occasional in June and in fall. Smith 1920.

Scenedesmus:

S. arcuatus Lemmermann. 8-celled colony 20 x 22 mu; cells 4-5 x 9-16 mu. Two- and four-celled colonies also present. Rare, in spring and fall. Smith 1920.

S. arcuatus var. *capitatus* G. M. Smith. Colonies 18 x 22 mu; cells 7-9 x 13-15 mu. Rare, in June and November. Smith 1920.

S. obliquus (Turpin) Kützing. Cells 2-2.5 x 7.8-10 mu; in clusters of 4 or 8. Rare, in May and January. Smith 1920.

S. armatus (Chodat) G. M. Smith. Cells 7 x 19 mu; spines 10 mu. One seen, in August. Smith 1920.

Crucigenia:

C. rectangularis (Nägeli) Gay. Cells 5 x 10 mu. Rare, September to November. Smith 1920.

Spirogyra:

Undetermined species. Cells 32 x 190 mu. Scattered, rarely, in warmer months. Smith 1920.

Netrium:

N. digitus (Ehrenb.) Itz. & Rothe. var. Length 300 mu; breadth 29 mu, chloroplast ragged; central pyrenoid large. This is somewhat narrower than the minimum (40 mu) given by West. One seen, in June. Smith 1924.

Closterium:

C. Venus Kützing. Length between apices 75-105 mu, breadth 6-12 mu. Often slightly twisted out of one plane. Rare, throughout the year, except summer. Smith 1924.

C. moniliferum (Bory) Ehrenb. Length between apices 295 mu; breadth 41 mu. One seen, in May. Smith 1924.

C. aciculare T. West var. *subpronum* W. & G. S. West. Length 550-650 mu; breadth 6.5 mu; often in floating bundles of 2-20. Occasional to very common in the colder months, October-February. Smith 1924.

Undetermined species, compare *pronum* Breb. Length 275-378 mu; breadth 7-8 mu; terminal space 45 mu; 5-6 pyrenoids per semi-cell; tips curving in same or different directions. Agrees in dimensions but not exactly in contour with the description of West. Scattered rarely throughout the year, especially in cooler months. West I 1904.

Pleurotaenium:

P. trabecula (Ehrenb.) Nägeli. Length 450 mu; breadth through central ridge 27 mu, at apices 22 mu. One seen, in June. West I 1904.

Cosmarium:

C. depressum (Nägeli) Lund. var. *achondrum* (Boldt) W. & G. S. West. Length 25-26 mu; breadth 28-29.5 mu; breadth of isthmus 8 mu. Occasional from May to July. Smith 1924.

C. contractum Kirchner var. *ellipsoideum* (Elfv.) W. & G. S. West. Length 23-28 mu; breadth 20-22 mu; breadth of isthmus 5-6 mu. Occasional in every month of the year but July. West II 1905.

Staurastrum:

S. dejectum De Brébisson. Length without spines 31 mu; breadth without spines 30, spines 3-4.5 mu; breadth of isthmus 6 mu. Rare, in spring. Smith 1924.

S. cuspidatum De Brébisson. Length without spines 36 mu; breadth without spines 38 mu; spines 10-12 mu; breadth of isthmus 6 mu. Occasional in June-July and October-November. Smith 1924.

S. pseudopelagicum W. & G. S. West. Length without processes 32 mu; breadth without processes 40 mu; breadth of isthmus 10 mu; terminal spines 6-7 mu. Like *S. paradoxum* but smaller, stouter, smoother, and with longer spines. Rare, in July. Smith 1924.

S. paradoxum Meyen. Length without processes 25-48 mu; breadth without processes 20-30 mu; breadth of isthmus 10-12 mu; great variation in shape. Rare in summer, occasional throughout other months of the year, rising to abundant in June. Smith 1924.

S. tetracerum (Kütz.) Ralfs. var. *trigonum* Lundell. Breadth with processes 40 mu. A small species with 3 or 4 minute terminal spines. Rare, in August, and in aquarium. Smith 1924.

Spondylosium:

S. planum (Wolle) W. & G. S. West. Length 12.2-16 mu; breadth 17-24 mu; breadth of isthmus 7 mu. Rare, in May-June and October-November. West V 1925.

DINOPHYCEAE

Peridinium:

P. divergens Ehrenberg. Diam. at girdle 62-75 mu; height with processes 70-80 mu. Identified by S. J. Eddy from preserved plankton samples. He states that "the species in this collection is *P. divergens,* a marine species. Apparently there must be brackish water in Lake Washington, because I have never seen this species or anything resembling it in strictly fresh water." Specimens were observed on seven dates from May to November, always rare. This species is probably not endogenous but is brought in accidentally by ships or log rafts from Puget Sound. Wailes 1928; Eddy 1930.

Ceratium:

C. hirundinella (O. F. Müller) Schrank form *brachyceroides* Schröder. Identified by S. J. Eddy. Length from tip to tip 200-275 mu; length of cyst from tip to tip 95 mu. Appearing occasionally from April to July, common in latter part of June; cysts in July. Schoenichen I 1925.

EUGLENOPHYCEAE

Phacus:

Undetermined species. 36-40 x 44-50 mu. Seen twice, in March and August. Smith 1933.

PROTOZOA

Tintinnus:

Species near *pinguis* Kofoid & Campbell. 38-40 x 84-110 mu. Thompson (1936, unpub. MS) proposes to call this *T. curtus*. His description: "Fresh-water species of Tintinnus; lorica subcylindrical, wider at the oral end than at the aboral end; 2.33-2.71 oral diameters in length; wall heavily rugose, with many agglomerate particles. Length 85-110 mu. The type locality is Lake Washington. . . . Occurs also in Black Lake, Cottage Lake, Peterson Lake, and South Lake, all in Washington. Common. Differs from *T. pinguis* in the absence of a median bulge." We found it rare to occasional in colder months, rising to very common in April; absent from June to October. Kofoid & Campbell 1929.

Tintinnopsis:

Species near *cylindrata* (Daday) Kofoid & Campbell. 34-37 x 71-160 mu. Thompson (1936, unpub. MS) proposes to call this *T. rugosa*. His description: "Fresh-water species of Tintinnopsis; lorica cylindrical in the anterior 0.75 of the total length; 2.54-4.5 oral diameters in length; oral rim entire, smooth; bowl beginning to taper in the posterior 0.25 of the total length, becoming narrowly rounded at the aboral end; wall heavily rugose with sub-uniform agglomerated particles. Length 85-180 mu. The type locality is Lake Washington. . . . Occurs also in Cottage Lake, South Lake, and Lake Union, all in Washington. Differs from *T. cylindrata* in greater size and different proportions of the aboral end." We found it rarer than Tintinnus in numbers; in all months but the warmer ones June to October. Kofoid & Campbell 1929.

Vorticella:

Species "A." Diam. cell 18-40 mu; diam. stalk without sheath 4.5-5 mu, with sheath 6-7 mu; length of stalk 10-45 mu. A small transparent species of the *microstoma* type, commonly attached to Anabaena, Stephanodiscus, and Botryococcus; single or in clusters. In all months of the year; common in the warmer months from May to September. Noland and Finley 1931.

Species "B." Diam. cell 40-125 mu. A larger, usually darker species of the *campanula* type; single or in clusters of up to 25. Appeared in May, became very common by July and disappeared in August. Noland and Finley 1931.

Epistylis:

E. flavicans Ehrenb. Cells 30 x 45-50 mu; diam. stalk 6-8 mu. Single or in large colonies. Occasional, May to July. Schoenichen II 1926.

Undetermined species. Diam. cells 28-30 mu; stalk 5.5 mu. In groups of 4-50, usually attached, as to the moults of copepods. Differs from *E. flavicans* in smooth, spherical contour; cell capsule thick, refractive, and apparently composed of 3 lamellae. Rare, in May and June.

Podophyra:

Undetermined species attached to copepods in July and August. 10-12 x 20-22 mu.

Cyst of a protozoan, possibly this genus. Height 35 mu; diam. 53-67 mu; thickness of rim 12 mu. Wall hyaline, crossed by faint striae, 5 circumferential in 10 mu. Rare, every month from February to July.

ROTIFERA

For the identification of the majority of species we are greatly indebted to Dr. Elbert H. Ahlstrom who examined material in formalin from all months of the year. To his list we were able to add but one species *(Trichocerca cylindrica)*; and one species reported by him as rare we did not encounter *(Brachionus calyciflorus)*. We quote from a letter from Dr. Ahlstrom: "The material contained the usual limnetic rotatoria and a few contracted Bdelloids which were impossible to identify. *Lepadella acuminata* and possibly *Diurella rousseleti* are adventitious, the others are truly limnetic species. None of the species is rare as far as world-wide distribution goes. *Ploesoma hudsoni* is found usually in deep, cold lakes, and is probably of more limited distribution than the other species. *Diurella rousseleti* has few records of occurrence for this country, though it is not as rare as the limited records would lead one to believe. The paucity of rotifers in the August 1 sample is hard to explain. In Lake Erie and Lake Michigan there is no August minimum. In Lake Erie the most common rotifers throughout the warmer months are *Polyarthra trigla* and *P. euryptera, Keratella cochlearis, Synchaeta stylata,* and *Filinia longiseta.* All Polyarthras in your material have the wide appendages characteristic of *P. euryptera. Notholca longispina,* the most common species in your material, is rare in Lake Erie, but rather common in Lake Michigan."

Collotheca:

C. mutabilis (Hudson). Body of female 36-50 x 70-147 mu. Eggs 24-26 x 32-40 mu. Occasional in June to August, otherwise rare; eggs June to November. Brauer 1912 (as *Floscularia mutabilis*).

Conochilus:

C. hippocrepis (Schrank). Body ca. 100 x 300 mu; two palpi. Occurring rarely from May to September, except in June, when increasing to occasional. Brauer 1912 (as *C. volvox*).

C. unicornis Rousselet. Differs from the preceding species in having one palpus instead of two, and in forming colonies of 2-25 instead of 60-100. The two species occur together, with *unicornis* appearing a trifle earlier in the summer. Brauer 1912.

Synchaeta:

S. stylata Wierzejski. Body of female ca. 60 x 85 mu; a crescent-shaped hyaline structure usually visible within. Rare to occasional from July to October. Brauer 1912.

Filinia:

F. longiseta (Ehrenberg). Body 65 x 107 mu; ant. spines 380, 400 mu; post. spine 315 mu. Two specimens were observed, June and July, both with ant. spines folded up out of normal position beside the post. spines. Brauer 1912 (as *Triarthra longiseta*).

Polyarthra:

P. euryptera (Wierzejski). Body of female ca. 100 x 170 mu; swimming appendages up to 26 x 130 mu. Occurring rarely throughout entire year, somewhat more common in July to October; egg noted in July. Brauer 1912 (as *P. platyptera* var. *euryptera*).

Diurella:

D. rousseleti (Voigt). Body ca. 30 x 80 mu; foot 30 mu. Occurring rarely throughout the year. Brauer 1912.

Trichocerca:

T. cylindrica (Imhof). Body 80 x 390 mu; foot 275 mu. A stray form noted once, in July. Brauer 1912 (as *Rattulus cylindrica*).

Lepadella:

L. acuminata (Ehrenberg). Body 48 x 97 mu; entire foot 51 mu; toe 38 mu. Two specimens seen, January and August. Brauer 1912 (as *Metopidium acuminata*).

Brachionus:

B. calyciflorus Pallas. One specimen seen by Ahlstrom, April. Brauer 1912 (as *B. pala*).

Keratella:

K. quadrata (Müller). Body with spines 40 x 58 mu; eggs 40-43 x 60-65 mu. Occurring rarely in every month from January to August; eggs noted June and July. Brauer 1912 (as *Anuraea aculeata*).

K. cochlearis (Gosse). Body of female with spines 67 x 180 mu; eggs 40 x 60 mu. In all months but September and October, very common in May

and June; eggs from April to August, especially in May. Brauer 1912 (as *Anuraea cochlearis*).

Notholca:

N. striata (O. F. Müller). Body with spines 85 x 125 mu. Seen twice, in January and April. Brauer 1912.

N. striata var. *acuminata* (Ehrenberg). Body with spines 85 x 145 mu. One seen, in April. Brauer 1912.

N. longispina (Kellicott). Body of female with spines 50-60 x 550-650 mu; eggs 45 x 90 mu. Rare to occasional in every month of the year; eggs noted in every month, especially June. Brauer 1912.

Ploesoma:

P. hudsoni (Imhof). L. 378 mu; width (dorso-ventral) 168 mu; entire foot ca. 200 mu; toes 63 mu; lorica sculptured. Noted twice, June-July. Brauer 1912.

P. truncatum (Levander). L. 400 mu; width (dorso-ventral) 250 mu; entire foot 245 mu; toes 66 mu. Noted twice, June, July. Brauer 1912.

CRUSTACEA

Diaphanosoma:

D. leuchtenbergianum Fischer. Length of female without spine ca. 0.9 mm. In all months but February and March; abundant only in summer and fall; the most common cladoceran in the plankton. Birge 1918.

Daphnia:

D. pulex (de Geer). Length of female without spine ca. 2 mm. Rare; July to October. Birge 1918.

D. longispina (O. F. Müller). Length of female without spine ca. 1.8 mm. Quite common from May to October, old individuals occasional in winter. Birge 1918.

Bosmina:

B. longispina Leydig. Length of female without spine ca. 0.46 mm. Occasional throughout the year, abundant for a rather brief period, in July Birge 1918.

Leptodora:

L. kindtii (Focke). Length of female without terminal spines ca. 9 mm. Rare; noted only twice, August, October. Birge 1918; Brauer 1909.

Epischura:

E. nevadensis Lilljeborg. Length of female without terminal spines 2.1-2.2 mm.; male 1.85 mm. In all months of the year, though abundant only from July to October. This species replaces Diaptomus quite largely during the summer months. Breeding adults most common in August. Birge 1918.

Diaptomus:

D. ashlandi Marsh. Length of female without terminal spines 1.25-1.35 mm.; male 1.15-1.2 mm. The male rt. antenna and the fifth foot agree with the description of Marsh except that the rt. endopodite of the fifth foot is nearly twice as long as the first segment of the exopodite, rather than equal. Very common in winter, increasing from February to a peak in April-May and almost disappearing by July. A much smaller pulse in October. Over a long period about equal in numbers to Cyclops, but more seasonal. This is a common form in the Great Lakes. Marsh 1929.

Cyclops:

C. viridis Jurine. Length of female without terminal spines 1.0-1.1 mm. Body length about as *C. bicuspidatus;* head region of *viridis* distinctly broader; no cuspidate depressions on furcal rami. Rare, July to October. Marsh 1929.

C. bicuspidatus Claus. Length of female without terminal spines 1.0-1.1 mm. The most constant crustacean in the plankton. Seasonal fluctuation was apparent at the shallower ends of the lake, where there was a July-August minimum. At Madison Park the total number remained constant, but there was a definite migration from the surface to the 60-30 meter level during the warmer months. A limnetic species characteristic of the Great Lakes. Marsh 1929.

Canthocamptus:

C. staphylinoides Pearse. Rare; a marginal form straying into the limnoplankton at almost any season of the year. Marsh 1929.

Pontoporeia:

P. filicornis Smith. Length of male with body straight ca. 6 mm. An amphipod taken occasionally in deep plankton hauls from July to February, though in no sense a plankton form. Year-round in the bottom mud. Adamstone (1928) lists two species of Pontoporeia as the only members of the genus in the United States: "The amphipods of the deeper waters of the Great Lakes, and also of some other lakes in northern United States and Canada, belong to two relict species of the genus Pontoporeia." These are *P. affinis* (Lindstrom) known as *P. hoyi* previous to revision by Birge and Juday in 1927; and *P. filicornis* Smith. "Specimens of *P. filicornis* have been taken on only a few rare occasions, the species apparently being confined to the deeper, colder waters of the lakes in which it occurs in contrast to *P. affinis* which has a wide range of distribution with regard to depth. Smith based the description on a single individual taken from Lake Michigan in 1870." It has been taken also from Lake Ontario and Lake Nipigon. Huntsman (1915) mentions the occurrence of *P. filicornis* from

dredgings in Lake Michigan at a depth of 40-60 meters. Juday and Birge (1927) discuss the amphipod as follows: "Pontoporeia and Mysis are two crustaceans which are of special interest because they belong to a group of fresh-water animals that are regarded as 'marine relicts.' . . . In general, these relict organisms prefer cold water, and most of them are found only in lakes which have a cool lower stratum that is well supplied with dissolved oxygen throughout the summer period of stratification. . . . Two theories have been offered to account for such a fauna in lakes. One is that these forms occupied the lake basins while they were still below the surface of the ocean; subsequent elevation of the land brought the basins above sea level, and the inflowing water gradually changed them to fresh-water lakes. These relict forms were able to withstand the change from salt to fresh water so that they continued to inhabit the lakes after they were formed. The other theory is that these animals migrated into the lakes from the ocean at the close of the last great glacial period . . . *Pontoporeia affinis* is found chiefly below a depth of 10 meters during the summer period of stratification in Green Lake, Wisconsin. It lives on the bottom in the deepest portion of the lake where the supply of dissolved oxygen may fall below 1 cc. per liter at certain times. The breeding season extends from December to May." (Green Lake is 68 m. [225 ft.] deep.)

The taxonomic status of the species of Pontoporeia has not been fully cleared up. It is possible that the Lake Washington form is merely a sex-variation of *affinis.* An examination of Lake Washington specimens showed the presence of males in December, January, February, March, and April; females during all months of the year except July and November, when neither sex was taken. Adamstone 1928.

Neomysis:

N. mercedis S. J. Holmes. Length of male with body straight ca. 7 mm. This species was first taken in 1895 from Lake Merced, California. It was not taken in sufficient numbers in Lake Washington to warrant any conclusion as to its seasonal abundance. It appeared scatteringly in the plankton during all months from July to January, at depths below thirty meters. No specimens were taken with samples of bottom mud. Juday and Birge (1927) discuss the habits of a related species as follows: "*Mysis oculata* var. *relicta* Loven is found in Green Lake and in Trout Lake, Wisconsin. It remains on the bottom in the deeper water during the daytime in summer, but migrates into the upper water at night, even coming to the surface. In Green Lake it is found in water which possesses only about 1 cc. of dissolved oxygen per liter at times. The breeding season extends from October to May." This species has been found in Lakes Superior and Michigan to a depth of 300 meters. Neomysis is a splendid source of food for plankton-gathering species of fish like the Little Redfish *(Oncorhynchus nerka)* and the Whitefish *(Prosopium williamsonii)* both of which occur in

Lake Washington. Professor Trevor Kincaid recalls an examination of the stomach of a redfish from Lake Sammamish in which the contents were found to consist entirely of the tightly-packed bodies of this crustacean. *Leptodora kindtii* is taken in a similar manner. Holmes 1896.

PELAGIC DIATOMS OF LAKE WASHINGTON

Unless otherwise specified all magnifications are x 780.

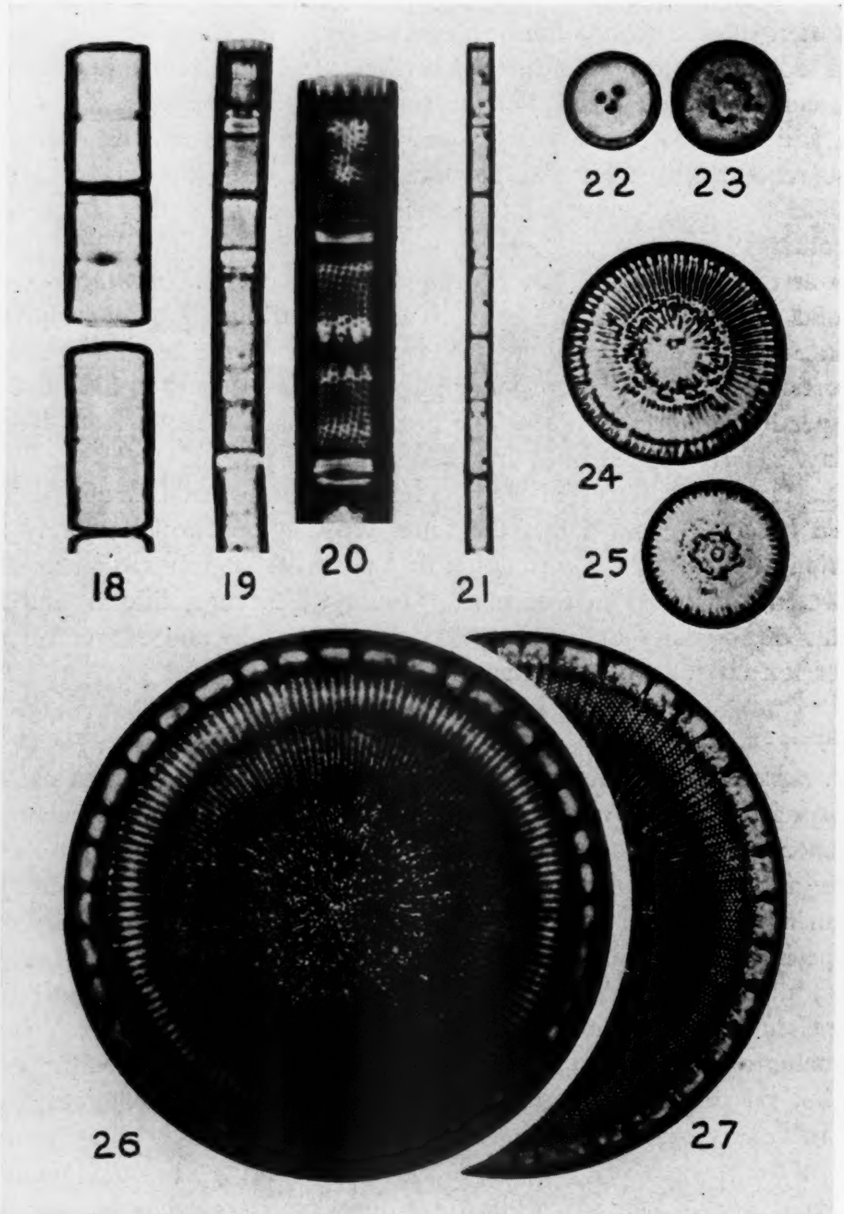

FIG. 18, *Melosira varians;* 19, *Melosira italica;* 20, *Melosira italica*, x 1560; 21, *Melosira italica* var. *tenuissima;* 22, *Cyclotella ocellata;* 23, *Cyclotella ocellata;* 24, *Cyclotella bodanica;* 25, *Cyclotella bodanica;* 26, *Stephanodiscus niagarae;* 27, *Stephanodiscus niagarae.*

PELAGIC DIATOMS OF LAKE WASHINGTON

Unless otherwise specified all magnifications are x 780.

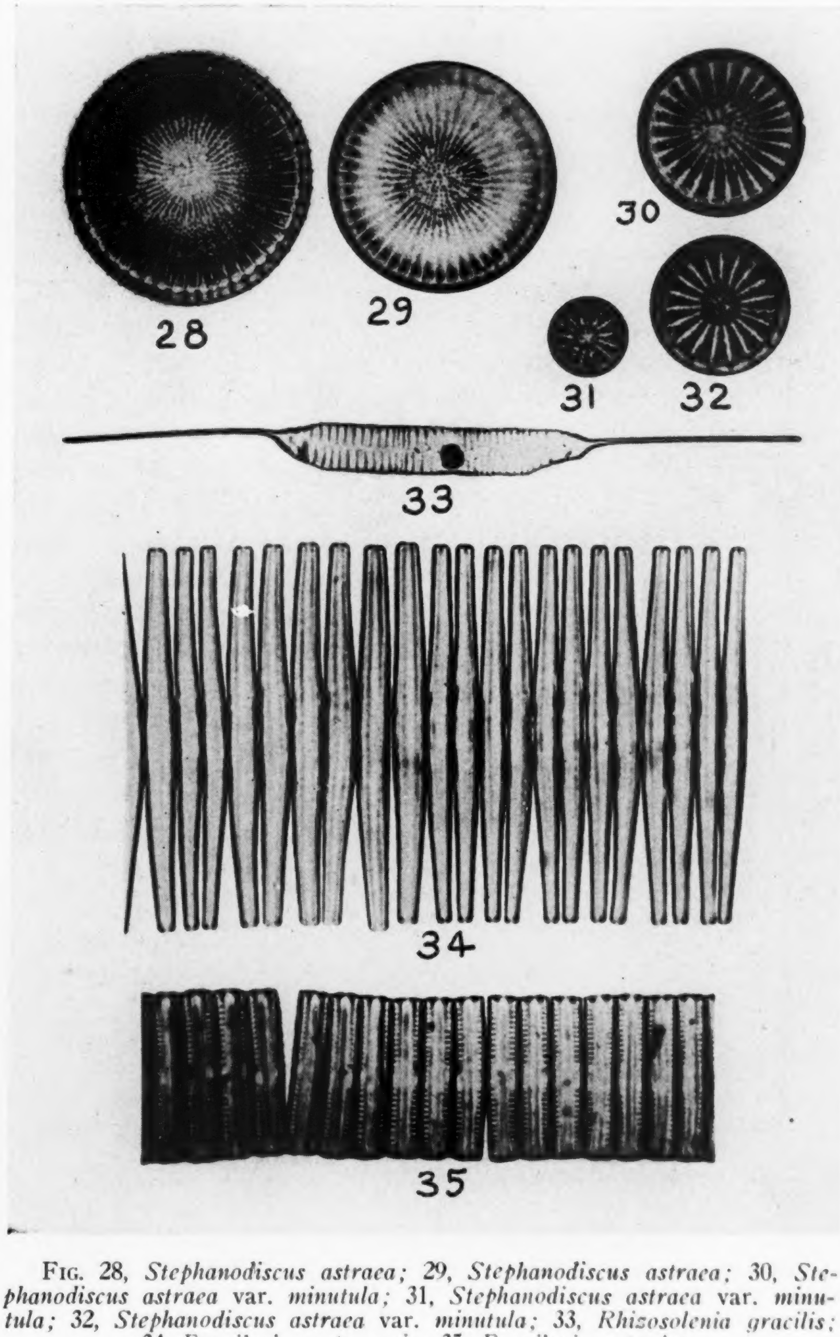

FIG. 28, *Stephanodiscus astraea*; 29, *Stephanodiscus astraea*; 30, *Stephanodiscus astraea* var. *minutula*; 31, *Stephanodiscus astraea* var. *minutula*; 32, *Stephanodiscus astraea* var. *minutula*; 33, *Rhizosolenia gracilis*; 34, *Fragilaria crotonensis*; 35, *Fragilaria capucina*.

PELAGIC DIATOMS OF LAKE WASHINGTON
Unless otherwise specified all magnifications are x 780.

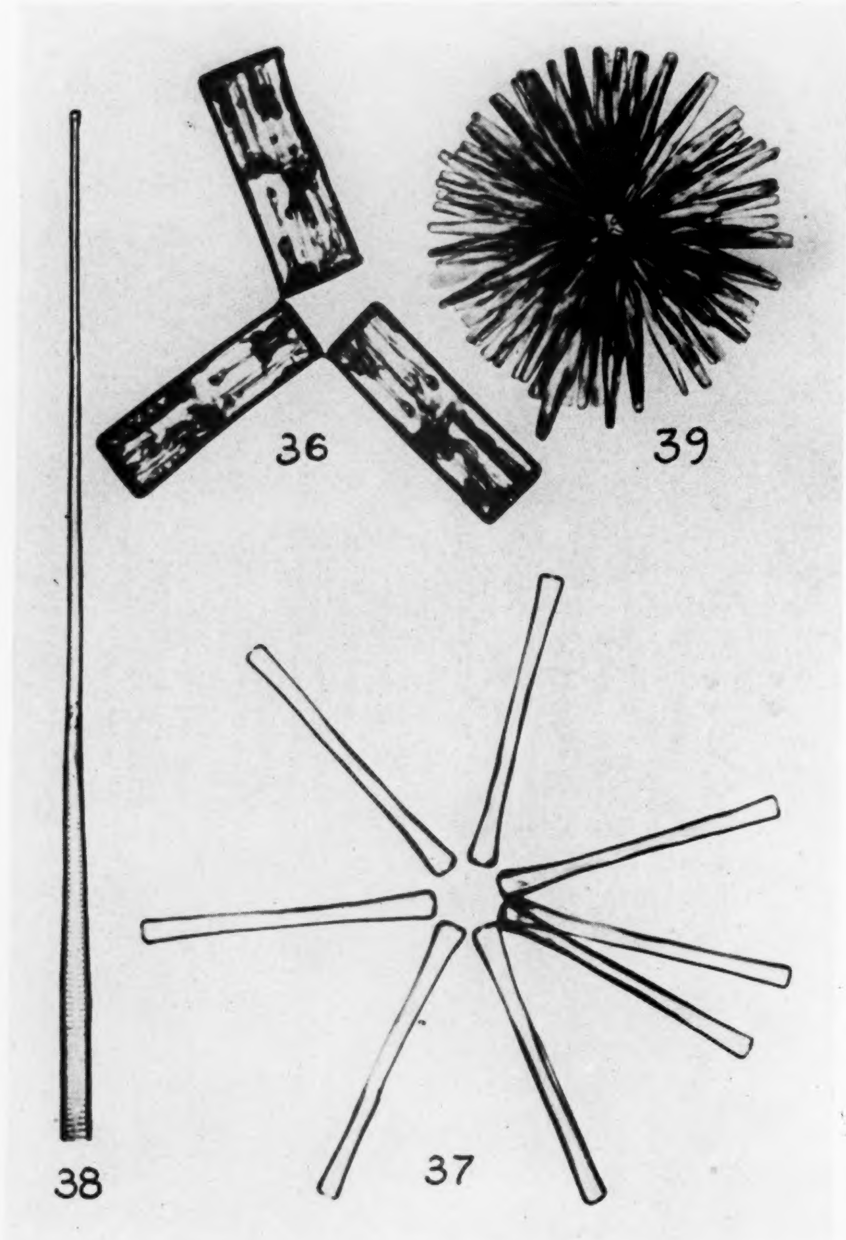

FIG. 36, *Tabellaria fenestrata;* 37, *Asterionella formosa;* 38, *Synedra ulna* var. *danica;* 39, *Synedra* sp.

SHORE AND BOTTOM LIFE

Brief mention is made of the occurrence of certain organisms in samples of bottom mud brought up with an Ekman dredge. The lake bottom is composed of smooth, very fine, gray to olive-brown silt, mixed with a slight amount of plant detritus, blackened fragments of leaves, fir needles and twigs. Organisms screened from this mud include midge larvae, oligochaetes, a single specimen of a leech, a small mollusc of the Sphaerium type, the ostracod Candona, and the amphipod Pontoporeia. All were taken at depths of from 30 to 60 meters. Midge larvae from 60 meters at Madison Park in all months of the year were identified by Prof. O. A. Johannsen as members of the Genus Procladius, probably *culciformis*, a common, widespread species. A few additional midge larvae from 30 meters at South Point were reported as Chironomus, group *decorus*. Ostracods taken at 30 meters off South Point in May were identified by Dobbin (1933) as *Candona caudata* Kaufmann. Miss Dobbin states that this is the first recorded occurrence in the United States.

The shore line of Lake Washington is relatively barren of vegetation, mainly due to the large size of the lake with resulting wind and wave action. The shoal areas are confined chiefly to the Sammamish River and Cedar River inlets, Meydenbauer Bay, Juanita Bay, and Mercer Slough. Twenty-one species of aquatic plants collected from these sites in August, 1936, were identified by Dr. George U. Jones as:

1. *Alisma plantago-aquatica* L.
   Water Plantain
2. *Elodea canadensis* (Michx.) Planch.
   Waterweed
3. *Azolla* sp.
4. *Callitriche palustris* L.
   Water Starwort
5. *Ceratophyllum demersum* L.
   Hornwort
6. *Hippuris vulgaris* L.
   Marestail
7. *Lemna minor* L.
   Duckmeat
8. *Lemna trisulca* L.
   Fairy Paddle
9. *Naias flexilis* (Willd.) R. & S.
   Slender Naias
10. *Nuphar polysepalum* Engelm.
    Yellow Pond Lily
11. *Potamogeton natans* L.
    Floating Brownleaf
12. *Potamogeton nuttallii* C. & S.
    Nutall's Pondweed
13. *Potamogeton pectinatus* L.
    Sago Pondweed
14. *Potamogeton pusillus* L.
    Small Pondweed
15. *Potamogeton richardsonii* (Benn.) Rydb.
    Richardson's Pondweed
16. *Sagittaria latifolia* Willd.
    Wappato
17. *Scirpus microcarpus* Presl.
    Small-fruited Bullrush
18. *Scirpus occidentalis* (Wats.) Chase
    Western Tule
19. *Sparganium greenei* Morong
    Branch-stemmed Bur Reed
20. *Typha latifolia* L.
    Cat-tail
21. *Vallisneria spiralis* L.
    Wild Celery (introduced)

SUMMARY

1. Data have been presented on the plankton and on the physical and chemical properties of the water in Lake Washington, King County, Washington, with a brief description of the land environment.

2. Lake Washington is the second largest lake in the State, with an area of 50 square miles and a depth of 214 feet. There are few shoal areas. It is of recent glacial origin with waters that have slowly been converted from salt to fresh.

3. On account of the mild, humid climate the lake never freezes. The water undergoes one long period of vertical mixing throughout the winter, in contrast to the two shorter ones characteristic of lakes that freeze over.

4. A thermocline appears in the summer, dividing the water body into an epilimnion which constitutes about 30% and a hypolimnion which constitutes about 60% of the entire body.

5. The annual heat budget in 1933 was 43,000 gram cal. per sq. cm., which is slightly higher than other lakes of the country at the same latitude.

6. Chemically speaking, the water of Lake Washington is soft, containing about 50-70 mg. dissolved solids per liter.

7. The oxygen content is relatively uniform at all depths. There is always at least 50% saturation at the bottom. A significant decrease occurs in the thermocline in late summer.

8. The carbon dioxide content shows a correlation with the oxygen and with the growth of plankton organisms. In 1933 a minimal value for free CO_2 of 0.7 mg/l. was found at the surface in August, while a maximum value of 6.10 mg/l. was found near the bottom on the same date.

9. The hydrogen-ion concentration remained fairly constant at a pH of 6.8 to 8.6. The epilimnion approximated neutrality or was faintly alkaline throughout the year.

10. The amount of ionic silicate fluctuated inversely with the growth of plankton diatoms. An average value of Si of 3 mg/l. in the epilimnion fell to as low as 0.8 mg during periods of active diatom growth.

11. Fluctuations in phosphate concentration were quite similar to those for silicate. Values ranged from none detectable to 0.025 mg/l.

12. The lake is relatively poor in nitrate as well as in phosphate. Nitrate ion ranged from 0.04 to 0.12 mg/l. Low concentrations were observed in the epilimnion during the summer months, possibly due to the presence of denitrifying bacteria.

13. Neither ammonia nor nitrite ion was present in an appreciable quantity.

14. The total amount of organic material in the lake water, as determined by several chemical methods of approach, was found to be about 1 to 2 mg/l. a value less than one-third that found by Birge and Juday in average Wisconsin lakes.

15. The plankton is quantitatively poor. In 1933 an average of 150 mg of dry net plankton per cu. m. was found. Of this the organic component averaged 58 mg/cu. m. On the basis of organic matter the plankton of Lake Washington is about 1/5 as rich as that of Lake Mendota, Wisconsin.

16. The plankton is so distributed vertically that more than 3/4 of the total amount occurs in the upper half of the water body.

17. Due to the dominant role of diatoms the dry plankton was composed of at least 50% ash during 8 months of the year. In mid-summer diatoms decreased to such a point that only 15% of the dry plankton was ash.

18. In the true limnetic plankton there were found 72 phytoplankters and 35 zooplankters, or a total of 107 species. In general, the population is similar to that of Lake Erie and Lake Superior, and unlike smaller lakes in the Puget Sound region.

19. The plankton complex, though varying from season to season, is known to be very stable over a period of at least 20 years.

20. The bottom fauna, though not fully investigated, seems to be characterized by the midge larvae Procladius and Chironomus; and the amphipod Pontoporeia. Corethra does not occur.

21. The littoral vegetation of the lake is scanty. Twenty species of aquatic spermatophytes and one pteridophyte are recorded.

22. On the basis of biological productivity as defined by Welch (1935) we conclude that Lake Washington is distinctly oligotrophic.

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